THE GROWTH AND DEVELOPMENT OF THE WINTER BARLEY CROP

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ABSTRACT

The growth and development of both six-row and two-row winter barley varieties was studied in field trials in two seasons near Edinburgh.

The rate at which the crop passed through development stages was closely related to temperature. For some aspects of development the date of sowing (ie photoperiod) was also important.

The agrochemical industry produces recommendations for applying hormonal chemicals based upon plant growth stage. Unfortunately external plant morphology could not be used as a guide to apical development; floral initiation occurred with as few as two or as many as five leaves unfolded on the mainstem.

Poor winter hardiness and leaf death were correlated with low levels of water soluble carbohydrate.

For all sowings the green area index (GAI) reached by the start of stem elongation was 1.0 ± 0.3. From this time until its maximum value the GAI increased linearly in thermal time.

Over much of the season crop growth rate was closely related to the rate at which photosynthetically active radiation (PAR) was absorbed. The six-row cultivars partitioned more dry matter to the ear than the two-row's, giving the six-row types a higher harvest index and higher grain yield.

Growing conditions before anthesis had a greater effect on grain yield than conditions afterwards. A positive correlation between absorbed PAR after anthesis and grain yield was not a causal relationship since it was based upon an increase in grain number rather than grain size.

There was little difference in the tillering behaviour of the six-row and two-row cultivars before mainstem elongation. Differences in final ear population were due to poor tiller survival in the six-row cultivars.

The number of viable florets at anthesis was more dependant on the proportion of spikelets aborted than upon maximum spikelet number. The percentage survival of spikelet primordia was positively correlated with the size of the two leaves below the flag leaf which were the main light intercepting organs during the period of spikelet death.

Grains appeared to reach their potential size since: the presence of sterile florets did not influence the size of neighbouring grains; grain size did not increase when there were unused stem reserves; and final grain weight on the mainstem was positively correlated with floret size at anthesis.

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Above all I am indebted to my wife, Smita, for her encouragement through the harder times of writing this thesis.

DECLARATION

This thesis has been composed by myself and all results presented are from my own studies.

David Grant

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All error bars are 95% confidence limits for the treatment mean except where stated otherwise. These are usually drawn on Athene for consistency.

LIST OF ABBREVIATIONS

CGR	-	Crop growth rate
Dr	-	Double ridge
Ds	-	Duration of initiation of spikelet primordia
Ff	-	The proportion of viable florets which are fertilised and set grain
GAI	-	Green area index
GAR	-	Green area ratio
GARGR	-	Green area relative growth rate
GS	-	Growth Stage
L1	-	The first leaf to unfold
L2	-	The second leaf to unfold
$L1^t$	-	The flag leaf
$L2^t$	-	Flag leaf -1
$L3^t$	-	Flag leaf -2
LAI	-	Leaf area index
LSD	-	Least Significant Difference
NIAB	-	National Institute of Agricultural Botany
PAR	-	Photosynthetically active radiation (0.40-0.70 μm)
RGR	-	Relative growth rate
Rs	-	Rate of initiation of spikelet primordia
S81	-	1981 sowing (sown 19 September 1980)
S82	-	1982 sowings (both S821 and S822)
S821	-	1982 - First sowing (sown 22 September 1981)
S822	-	1982 - Second sowing (sown 14 October 1981)
Sf	-	The proportion of spikelet primordia surviving to form florets at anthesis
SLA	-	Specific leaf areas
SMD	-	Soil moisture deficit
TC	-	Coleoptile tiller
T1	-	Tiller in the axil of the first leaf
T1P	-	Primary tillers from the T1 tiller
T1S	-	Secondary tillers from the T1 tiller
TM	-	Triple mound
ULR	-	Unit leaf rate
WSC	-	Water soluble carbohydrate

$$\text{Ear fresh weight per spikelet} = \frac{\text{total ear fresh weight}}{\text{number of viable spikelets}}$$

CHAPTER I

INTRODUCTION

In the Middle Ages, spring barley dominated the barley acreage in European countries. The winter barley acreage has increased only in the 20th century, particularly in the last 40 years to a position where it is now more widespread than spring barley in Continental Europe (Aufhammer, 1980).

The main reason for this change has been the yield advantage of winter sown barley over spring sown barley in the Continental climate. In West Germany, winter barley has out-yielded spring sown barley by an average of 24 per cent between 1950 and 1980 (Aufhammer, 1980).

In England and Wales the yield advantage over spring barley is smaller (around 5 per cent in NIAB[1] trials 1975-82), the difference being greatest in dry summers, though in some years spring barley can out-yield winter barley (Mann, 1982). However, the winter barley acreage has increased dramatically in England and Wales from 180,000 hectares in 1977 (10 per cent of the total barley area) to settle around 880,000 hectares (49 per cent of the total).

In Scotland, which has better yields of spring barley than England, the changeover to winter barley has been more recent. There was very little winter barley in Scotland in 1976, yet by 1983 it had 70,000 hectares (20 per cent of the total barley acreage) and this area is still increasing by about 20 per cent per annum. In Scotland, winter barley has been adopted more for its early harvest and reduction of spring labour requirements, than for any yield advantage. However, winter barley introduces the risk of winter kill and increased disease and weed problems.

Some of the presently recommended winter barley cultivars in Britain are of the six-row ear type, whilst all commercial spring barleys in the country are two-row. The highest yielding winter cultivars are six-rowed and these are also the most winter hardy. Most of our present winter barley varieties originate in

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[1]National Institute of Agricultural Botany.

Continental Europe where six-row barleys are favoured. In France, 45 per cent and in Germany, 60 per cent of the winter barley area is sown to six-row cultivars, whereas in the United Kingdom six-row varieties occupy only 10 per cent of the winter barley area (Lidgate, 1981). Despite six-row yields, which are around 5 per cent higher than two-row yields (Aufhammer, 1980) the six-rows are not preferred by farmers in the UK because of a tendency for ear loss if left ripe in the field, and poor grain quality characteristics. It is interesting to note that six-row barley was introduced to Northern Europe some 3000 years before two-row barley (Briggs, 1978) yet six-row types are largely unacceptable to farmers in Britain today.

The scientific literature relating to barley has been comprehensively reviewed by Briggs (1978) however it is worthwhile emphasising some aspects of growth and development.

The analysis of crop growth and development in cereals has, understandably, been aimed at increasing yield. Researchers first concentrated upon the components of yield (Engledow & Wadham, 1923), an aspect which has continued to receive much attention but which in isolation achieves little in understanding the fundamental causes of yield variation.

The concepts of growth analysis, (Gregory, 1917; Blackman, 1919; Briggs, Kidd & West, 1920) and their application to field crops (Watson, 1952) focused attention on whole crop growth (increase in dry weight) and photosynthetic area. Particular emphasis was given to the post-anthesis period following Archibold's demonstration that grain growth was largely based on current photosynthesis (Archibold, 1945). For a recent review see Thorne (1974).

Much of this work, based upon the traditional concepts of growth analysis, is limited by examining the crop as a closed system without adequate reference to the environmental control of crop growth and development. In contrast, a basic concept of crop physiology is that the crop responds to the prevailing environment and its ability to respond has been influenced by the preceding environment. Only recently has the whole crop been studied in conjunction with full

environmental recording (Biscoe *et al.*, 1975a; Gregson & Biscoe, 1975 ; Biscoe, Scott & Monteith, 1975b; Biscoe *et al.*, 1975c; Gallagher, Biscoe & Scott, 1975; Gallagher, Biscoe & Scott, 1976; Biscoe *et al.*, 1977).

One of the results of this work has been the adoption by some workers, of thermal time rather than chronological time, in describing crop growth. This makes comparison between environments easier since plants perceive time as a function of temperature (Monteith, 1981). Using thermal time is of greater importance when studying winter cereals which experience a wider range of temperatures than spring sown crops.

Regarding crop growth as responding to thermal rather than chronological time, has implications for recording crop development. Total growth is limited by the time taken to pass through development from sowing to maturity; lower temperatures delay development more than growth so that total yield is increased (Dobben, 1962; Äyräväinen & Paatela, 1974). In the field conditions generally experienced in Britain, the beneficial effects of lower temperatures in increasing the duration of growth, are greater than the adverse effects on crop growth rate (Monteith, 1981). The longer growing season for winter sown barley is probably the major reason for its higher yield than spring barley, since present spring cultivars can out-yield winter cultivars in certain situations when autumn sown (Ellis & Russell, 1984). Sowing winter barley early in the autumn similarly increases the duration of growth and usually gives higher yields of dry matter (Pfeiffer, 1949; Sage & Roffey, 1981; Sage & Roffey, 1982). However, sowing too early can lead to reduced final yields if development is rapid in the autumn and subsequent growth in the spring proceeds during low levels of insolation (Kahnt & Kubler, 1981). It is therefore evident that studies of dry matter productivity and partitioning need to be combined with studies of plant development.

Development in wheat, and presumably barley responds linearly to temperature before emergence and after anthesis (Angus *et al.*, 1981a; Angus *et al.*, 1981b; Porter *et al.*, 1981). For most crop

species, including barley, the rate of development between emergence and anthesis depends on photoperiod as well as temperature. Barley varieties differ in their response to photoperiod (Yasuda, 1982; Thompson & Matthews, 1982; Aspinall, 1966) and in general have a far weaker response than wheat, oats and rye (Dobben, 1962). In some cultivars the developmental response to day length is not a photoperiodic effect, but due to the extra solar radiation in longer days (Thompson & Matthews, 1982). Varieties also differ in their developmental response to temperature (Äyräväinen & Paatela, 1974).

Relating crop growth to solar radiation absorption rather than photosynthetic area has been used as an alternative to growth analysis measurements of unit leaf rate (ULR) based on leaf area alone. This enables valid comparisons of different crops or seasons to be made (Gallagher & Biscoe, 1978). Several workers have shown that crop growth rate is in fact proportional to the amount of photosynthetically active radiation (PAR) absorbed for a given period (Gallagher & Biscoe, 1978; Hawkins, 1982).

Photosynthesis normally operates on the linear portion of the irradiance response curve at irradiances experienced in Britain, once a full canopy has formed (Gallagher & Biscoe, 1978). However, barley leaves can be light saturated, both before a full canopy has formed (Iwaki, Takeda & Udagawa, 1976; Fukai, Koh & Kamura, 1976) and after anthesis in a sparse crop at high irradiances (Biscoe *et al.*, 1975c) which will reduce the amount of dry matter produced per MJ of PAR absorbed. The situation after anthesis is complicated further by the effects of ageing on photosynthesis (Gallagher, 1976). Air temperatures between 10°C and 25°C have very little effect on the rate of photosynthesis of temperate crops in the field (Murata & Iyama, 1963). Air and soil temperatures below 10°C can depress photosynthesis in field grown barley (Takeda, 1979) and the rate of photosynthesis can remain depressed following night frost despite non-limiting air temperatures (Iwaki, Takeda & Udagawa, 1976; Fukai, Koh & Kamura, 1976). Following these observations, Takeda (1982) suggests a simplified model of the response of photosynthesis to low temperature in which photosynthesis is optimal (= 1.0) between 15°C and 25°C with a linear reduction to 0.8 x optimal at 10°C, 0.5 x optimal at 5°C, and 0.1 x optimal at 0°C. Monteith (1981) suggests

a linear reduction in the rate of photosynthesis from an optimal level at 10°C to zero at 0°C.

The amount of PAR absorbed is dependant on the seasonal variation in both GAI and PAR. The pattern of GAI development is important both early and late in the season, since at a GAI of about 3 the crop intercepts about 70 per cent of the possible PAR (Gallagher & Biscoe, 1978). Thus any factors which limit leaf expansion before this GAI is reached are of particular importance in limiting crop dry matter production. Canopy development before stem elongation, is dependant on leaf appearance, expansion and senescence.

Several workers have found that the rate of leaf appearance is linear in thermal time (Gallagher, 1976 ; Baker, Gallagher & Monteith, 1980 ; Ellis & Russell,1984 ; Kirby, Appleyard & Fellows, 1982 ; Hay & Tunnicliffe-Wilson, 1982). This relationship appears to hold, except when severe cold restricts the rate of leaf extension (Hay & Tunnicliffe-Wilson, 1982). The later that a cereal crop is sown in the autumn the faster its leaves emerge per degree day, and it has been suggested that the rate of appearance is better correlated with the rate of change of day length at crop emergence, than with mean day length when the leaves are appearing (Baker, Gallagher & Monteith, 1980 ; Kirby, Appleyard & Fellows, 1982 ; Hay & Abbas Al-Ani, 1983 ; Ellis & Russell, 1984).

Winter barley has low rates of leaf extension per degree day during winter, possibly because of an interaction between low temperatures and short day length (Kirby, Appleyard & Fellows, 1982). Leaf expansion is dependant on the photosynthetic activity of existing leaves (Felippe & Dale, 1973) and leaf size could be limited by any reduction in assimilate production caused by cold stress or snow cover in winter.

Loss of green area due to leaf senescence and plant death can have a greater influence on the GAI of winter cereals than any environmental control of leaf expansion and appearance.

Over-wintering cereal plants are subject to a number of stresses which singly, or in combination may be lethal. The environmental stresses causing winter injury are not necessarily related to low

temperature *per se*, but to the sequence of temperatures, snow, ice, flooding, and soil and crop conditions. The susceptibility of plant tissue to low temperature is dependant on the degree of hardening, tissue age, and physical protection from the environment.

Hardening of winter cereals proceeds in two stages; first, exposure to low positive temperatures; and then subsequent exposure to slight negative temperatures (Trunova, 1982; Dantuma & Andrews, 1960). Hardiness declines after about a month at low temperatures (Jenkins & Roffey, 1974). Winter barley does not harden as well as wheat or rye (Barashkova & Alekseeva, 1980). Barley varieties differ in their pattern of hardening, for example, the two-row variety Maris Otter is very susceptible to frost after 11 days at low temperatures but only moderately susceptible after 25 days, whilst the six-row variety Astrix is extremely hardy at 25 days but less hardy than Maris Otter at 11 days (Jenkins & Roffey, 1974).

Many biochemical, morphological and physiological changes are known to occur in plants during cold hardening (Gusta, Fowler & Tyler, 1982; Levitt, 1972). These changes are more pronounced in winter than spring barley cultivars (Havaux & Lannoye, 1982). However, it is difficult to establish which changes cause hardening, and the correlation of a plant constituent with hardening may only be good when it is the limiting factor in the hardening process. Low temperatures lead to an accumulation of sugars during cold hardening in cereals primarily due to the excess of photosynthesis over growth (Levitt, 1972). Sugars protect sensitive tissue , stabilise the membrane structure and decrease cell dehydration (Trunova, 1982). Winter barley reduces its rate of photosynthesis in response to low temperatures more than winter wheat, which may account for the poorer frost hardiness of barley (Kaul & Reisener, 1981). Carbohydrate levels in the autumn are important for developing and sustaining cold hardiness, and for disease resistance; maintenance of carbohydrate reserves is important for recovery and growth in the spring. However, plants which do not acclimatise also increase their carbohydrate content in response to low temperatures, so although carbobydrate accumulation appears essential for cold hardiness it is not likely to be the only mechanism involved (Chen & Li, 1982).

The observation that the capacity to store assimilate in the grains may limit grain yield as much as the capacity of the crop to provide assimilate during grain filling (Yoshida, 1972; Evans & Wardlaw, 1976), and recent work showing that storage reserves make a variable contribution to yield (Stoy, 1980) has led to a greater emphasis being given to whole crop growth, and partitioning of dry matter to those organs which will eventually determine grain yield.

The proportion of total yield which is harvested as grain, depends upon the rates of distribution and redistribution of photosynthate to various organs. Comparisons of modern with older cultivars of both wheat and barley show that the major advances in grain yield are due to a higher harvest index rather than a greater total dry matter yield (Austin *et al.*, 1980a; Riggs *et al.*, 1981).

The allocation of assimilate to different organs is governed by their relative demand for carbon which is largely determined by the crop development stage and environmental conditions, especially temperature. Soluble and storage carbon forms a higher percentage of plant weight, relative to structural carbon, at 10°C then at 20°C or 30°C (Farrar, 1980). At all temperatures, the relative growth rate of particular organs of vegetative barley seedlings remains constant while the carbohydrate content of the plant varies; this suggests that the growth of each organ is more dependant upon its demand, than the availability of storage carbon (Farrar, 1980).

The grain storage capacity is a function of the number of ears per unit area, grains per ear and potential grain weight. In a multiculm barley plant, the ear population is dependant on tiller production and survival.

Rapid growth of a tiller bud in barley, is unable to occur until it has formed vascular connections with the leaf above (Fletcher & Dale, 1974). Hence, tillers are dependant on the supra-axillary leaf for carbohydrate until the tiller leaves have emerged, and on the rest of the plant for nutrients and water until their nodal root system is established. The rate of tiller growth is controlled by the available PAR (Willey & Holliday, 1971; Feltcher & Dale, 1974; Andersen, 1955) the available moisture

(Lawlor *et al.*, 1981) and the nutrient supply, especially nitrogen (Fletcher & Dale, 1974 ; Aspinall, 1961) all of which are affected by intra-plant competition (Willey & Holliday, 1971). The competition for assimilate and nutrients between tillers and mainstems is not equally balanced (Fletcher & Dale, 1974). There appears to be hormonal control over the distribution of metabolites in favour of the mainstem, giving a degree of apical dominance, which seems to be greatest during stem elongation (Jewiss, 1972 ; Langer, 1979).

Tiller emergence occurs in two phases with a cessation during stem elongation (Aspinall, 1961). The duration of tiller emergence in the first phase can be prolonged by factors that delay stem elongation in the mainstem (Kirby & Faris, 1970 ; Fairey, Hunt & Stoskopf, 1975). There is no evidence in the literature of tillers emerging from rapidly elongating shoots, but barley plants can continue to produce tillers despite mainstem elongation, if nutrients, moisture and light are not limiting, presumably by secondary tillering on low order tillers which are not themselves elongating (Aspinall, 1961). In field crops, tillering stops either before or soon after the start of stem elongation on the mainstem, due to intra-plant competition.

The same factors which promote initial tiller growth also encourage tiller survival (Lawlor *et al.*, 1981 ; Austin & Jones, 1975 ; Simpson, Lambers & Dalling, 1982).

The number of grains per ear is determined by the rate and duration of spikelet primordia initiation on the ear and the proportion of spikelets which survive to produce grain (Gallagher, Biscoe & Scott, 1976). Barley varieties are known to differ considerably in their response to environmental control of grain number per ear (Tingle, Faris & Ormrod, 1970).

Archibold (1945) pointed out that most material for grain growth is produced after anthesis. However, the maximum grain size may be determined earlier. It has been found that the rate of dry matter accumulation during the linear phase of grain growth is positively correlated with initial caryopsis size in barley (Scott *et al.*, 1983). This relationship produced a significant correlation between final grain weight and floret weight at anthesis, both between

varieties and different grain positions on the ear (Scott *et al.*, 1983). Similar correlations between average dry matter per floret and final grain weight have been reported for wheat (Fischer & Lambers, 1978).

Experiments involving grain removal after anthesis can lead to a slight, though not fully compensatory increase in the size of remaining grains (Prince, 1976 ; Martinez-Carrasco & Thorne, 1979 ; Walpole & Morgan, 1973). However, demand from the ear influences the speed of assimilate flow to the ear, and grain removal decreases this flow in wheat and presumably barley (Wardlaw & Moncur, 1976). This control of assimilate flow by the sink may result in no increase in the final grain weight of remaining grains when the number of grains per ear is reduced (Buttrose & May, 1959 ; Nösberger & Thorne, 1965). Control of assimilate supply in both the lag and linear phase of grain growth can also have some effect upon final grain size. Shading or severe moisture stress in the immediate post-anthesis phase can limit final grain size by reducing the capacity of the endosperm to accumulate starch (Jenner, 1979 ; Aspinall, Nicholls & May, 1964). Crop thinning in this period may also increase final grain size under certain conditions (Gallagher, 1979b; Herzog, 1982). However, the longevity of photosynthetic capacity or the availability of incident PAR does not always influence the final grain size of barley under field conditions in Britain (Willey & Holliday, 1971).

Carbohydrate for grain filling can come from several sources. The interception of solar radiation by the upper organs, their favourable situation for translocation to the ear and their youth relative to lower leaves means that the majority of post-anthesis assimilate in barley grains comes from the flag leaf, sheath and ear, under normal conditions (Biscoe *et al.*, 1975c). The relative contributions of the various organs depends, to a large extent, on the supply provided by other organs and sink demand. Movement of assimilate appears to be regulated by the proximity and size of sinks (Hozyo & Kobayashi, 1969). A study of several spring barley cultivars showed leaf photosynthesis to contribute 95 per cent of total canopy photosynthesis during stem elongation, falling to

41 per cent, two weeks after anthesis (Austin *et al.*, 1977). Stem reserves can also contribute to grain filling (Biscoe *et al.*, 1975c). It is not known if differences in the source of carbohydrate, between cultivars or seasons, affects grain yield (Thorne, 1974).

The relatively rapid adoption of winter barley in Britain has meant that little research has yet been undertaken specifically on winter sown barley. Most of the recent cereal research has been carried out on wheat or two-row spring barley. However, winter and spring barley cultivars are genetically very similar, and some of the present 'winter' barley cultivars are of alternative type. Field trials have revealed few differences between the types (Ellis & Russell, 1984; Russell *et al.*, 1982). However, they often differ in specific phenological responses to the environment due to their selection from separate gene pools in different environments (Yasuda, 1982). Winter cultivars usually have a vernalisation requirement and are more likely to have a long day response for flowering, though the most important qualification for winter cultivars is the ability to withstand low temperatures. These differences may be confounded by any differences between the six-row and two-row types, as both have to be studied in relation to autumn sowing.

Numerous yield trials (MAFF, 1970-80) and some development studies (Barling, 1980b) have enabled recommendations to be made for growing winter barley (MAFF, 1979; SAC, 1980). However, the literature investigating aspects of growth and development in winter barley is limited (eg Russell *et al.*, 1982; Ellis & Russell, 1984; Kirby, Appleyard & Fellows, 1982; Kahnt & Kubler, 1981; Penchev, 1981; Barling, 1980b; Fukai, Koh & Kamura, 1976; Sage & Roffey, 1981; Sage & Roffey, 1982). Comparisons between six-row and two-row cultivars are even rarer (eg Äyräväinen & Paatela, 1974; Äyräväinen, 1976; Riggs & Kirby, 1978; Kirby & Riggs, 1978; Williams & Hayes, 1979; Tingle, Faris & Ormrod, 1970). None of these provide a comprehensive description of field grown winter barley.

The present study was therefore planned to gain an understanding of the growth and development of the winter barley crop in South East Scotland so that its response to changes in environment or management might be predicted.

CHAPTER II

EXPERIMENTAL CROPS, MEASUREMENTS AND TECHNIQUES

Studies were made of winter barley grown in field trials according to standard agricultural practice. Both six-row and two-row cultivars were grown for comparison. The environmental control of growth and development was studied by having trials at three sowing dates.

2.1 Experimental Treatments, Sites and Crop Husbandry

Winter barley varieties were grown in field trials during 1980-81 and 1981-82. Three varieties: Maris Otter, Video and Athene were used in the first year; and four in the second: Maris Otter, Igri, Athene and Gerbel.

Athene is an early ripening six-row barley with a very high yield potential and good winter hardiness (breeders - Eckendorf, Germany FDR). It was the first six-row variety to be included in the recommended list by the National Institute of Agricultural Botany (in 1977) and the Scottish Agricultural Colleges. At the time of the trial it was the only six-row variety being grown commercially in Scotland.

Video is a two-row variety of moderate yield potential (breeders: Ackermann, Germany FDR). In 1980, it was under consideration for recommendation by the NIAB, but was not adopted since it showed no improvement over its parent Igri.

Maris Otter was the only winter barley variety recommended as suitable for malting by the NIAB in 1980-82. It is a two-row variety of alternative winter spring type, selected from a cross of Proctor and Pioneer by the Cambridge Plant Breeding Institute, and first recommended by NIAB in 1965. It was not recommended by the Scottish Colleges due to its poor winter hardiness.

In 1981-82 another six-row variety was introduced for comparison with Athene, and Video was replaced by its parent Igri, which then occupied most of the winter barley acreage in Britain.

Igri is a high yielding, two-row barley (breeders: Ackermann, Germany FDR). It has good winter hardiness and was the only two-row winter barley variety recommended for growing in Scotland at the time of the trial.

Gerbel is a six-row variety with a very high yield potential and good winter hardiness (breeders: Desprez, France). Athene and Gerbel were the only six-row varieties recommended by the NIAB in 1981.

Particulars of the treatments, sites and husbandry are presented in Tables 2.1a and 2.1b. In 1980, the trials were sown in trial plots on the Bush Estate, about 20 km south of Edinburgh. The varieties were sown with a 'Wartsila Falcon' seed-drill with 11.4 cm row-spacing in plots of 10 rows x 15.4 m. The weight of seed sown was not adjusted for variety which resulted in different plant populations. The plots were protected from rabbit damage over the winter.

In 1981, the trial was sited within a commercial crop of Igri winter barley on Boghall farm. These plots were about 1.5 km east of the previous trial. The commercial crop was sown before and harvested after the experimental plots. Individual plots of 21 rows x 12 m were sown with the Wartsila drill. The amount of seed sown was adjusted for variety to achieve a target population of 450 viable seeds per square metre, assuming 90 per cent germination.

The crop husbandry policy, was to follow normal agricultural practice (SAC, 1980) except that when a particular treatment was required on a single variety, all varieties received the application.

2.2 Crop and Plant Measurements

The 'functional' approach to field experimentation with small, yet frequent, harvests was chosen in preference to the 'classical' approach with a series of large infrequent harvests, in order to gain a fuller understanding of crop growth and development. Such an approach facilitates computer analysis and the study of changes with time, rather than direct comparisons at a single harvest (Hunt, 1978).

TABLE 2.1a: Details of the experimental treatments

	1980-81 (S81)	1981-82 (S82)
Variety	Athene six-row M. Otter two-row Video two-row	Gerbel six-row Athene six-row M. Otter two-row Igri two-row
Sowing dates	S81: 19 September	S821: 22 September S822: 14 October
Seed thousand grain weight (g)	Athene: 55 M. Otter: 38 Video: 55	Gerbel: 45 Athene: 45 M. Otter: 35 Igri: 48
Sowing rate	Rate not adjusted for variety; drill set at 190 kg ha^{-1} for variety Igri	Rate adjusted for variety to give 450 viable seeds m^{-2} assuming 90 per cent germination
Initial mean plant population at full emergence (plants per m^2)	Athene: 160 M. Otter: 230 Video: 160	S821 / S822 Gerbel: 450 / 440 Athene: 410 / 430 M. Otter: 440 / 450 Igri: 460 / 430
Final harvest	3 August	4 August
Replicates	4	4
Plots	12	32
Design	Completely randomised	Randomised block

TABLE 2.1b: Details of the experimental sites and husbandry

	1980-81 (S81)		1981-82 (S82)	
Trial site	55° 51' N, 3° 12' W		55° 51' N, 3° 11' W	
UK Ordnance Survey 1 inch sheet National Grid Ref;	NT 634245		NT 638260	
Altitude	185 m		168 m	
Soil type	Darvel Series: Freely drained sandy loam overlying sand subsoil		Winton Series: Imperfectly drained sandy clay loam till, overlying gley clay loam subsoil	
Soil analysis:	Dec 1979	Feb 1981	Dec 1979	Dec 1982
pH	6.3	6.0	6.2	6.2
P mg kg^{-1}	9.5	10.4	5.3	5.2
K mg kg^{-1}	70	91	42	51
Mg mg kg^{-1}	93	83	260	227
Previous crop: 1979	Sugar beet		Permanent pasture	
1980	Fallow		Spring barley	
1981			Spring barley	
Seedbed fertiliser	251 kg ha^{-1} of 15:15:21		350 kg ha^{-1} of 8:24:24	

Continued

TABLE 2.1b: (Continued)

		1980-81 (S81)		1981-82 (S82)	
			Date of Application		Date of Application
Nitrogen applied kg ha^{-1} at stated growth stage[1]. Seedbed (as above)		38	19/9/80	28	21/9/81
	12-14	-	-	40	25/2/82
	17	55	2/4/81	-	-
	31	-	-	50	S821 only 20/4/82
	31	-	-	50	S822 only 28/4/82
	31-32	55	21/4/81		
Herbicide applied at recommended rate. Growth stage:	13	Brittox	4/12/80	-	-
	31	-	-	Brittox	20/4/82
Fungicide applied at recommended rate. Growth stage:	13	Bayleton	4/12/80	-	-
	18	Bavistin FL	8/ 4/81	-	-
	31	-	-	Tilt MBM	20/4/82
	41-49	Bayleton BM	20/ 5/81	-	-
	65-75	-	-	Mistral	18/ 6/82
Manganese sulphate applied at growth stage: 35-41		-	-	5 kg ha^{-1}	20/ 5/82

[1] All growth stages are from the decimal growth code (Tottman & Makepeace 1979).

2.2.1 Field observation

Plots were observed at least weekly. Scores were recorded for: growth stage, pest damage, disease, weeds and the state of the crop. The decimal code for growth stages was used throughout the study; (Tottman & Makepeace, 1979).

Specific areas were marked out in each plot to record crop and ear emergence (500 mm x 2 rows in S81, 500 mm x 4 rows in S82). The dates of 50 per cent seedling emergence were recorded in S82 only, from several counts of plant numbers within these areas, during the period of emergence. The dates of ear emergence were acquired in the same way. The date of anthesis was estimated from the ear emergence counts and observation of the timing of anthesis relative to ear emergence in individual ears.

During the 1981-82 winter, crop damage was recorded in the marked out areas. Observations were made at weekly intervals (and after severe weather) to record: plant death, mechanical damage, leaf and tiller senescence and visible stress.

2.2.2 Destructive sampling

Harvesting procedure

Sequential weekly harvests formed the basis of sampling in both years. Harvests were missed if crop growth and development were chronologically slow, such as in winter. When severe weather (snow cover, frozen soil, heavy rain) prevented harvest at the appropriate time, the harvest was delayed until conditions had improved.

One sample area of 500 mm x 2 rows was chosen at random in each replicate for harvesting. Two 'guard' rows were left between sample areas. The plants were harvested with a trowel or by pulling, depending on plant size, and placed in polythene bags.

In the S82 trial, the sample area was harvested in two sections, with approximately one-third of the sample dug up to trowel depth (about 100 mm) to retain the roots and soil, the rest being harvested as usual. Harvesting of roots continued until the plants reached growth stage 31 (GS31).

A further sample of five or six plants was harvested adjacent to the main sample area, to be used for plant dissection. All samples were then taken to the laboratory for analysis.

Samples were processed in replicate batches, those not immediately required were stored in a refrigerator at 2°C to prevent deterioration. For the S82 trial the sample with roots was washed to remove soil and debris and roots cut from the shoots. Washed roots were then left for 24 hours in cold water to allow inorganic and dead organic material to separate out. The shoots of plants in this subsample were processed separately, to determine the ratio of root to total harvested dry weight.

Population counts

The number of plants, live stems, emerged ears, and bird-damaged ears were recorded on the main sample at the appropriate time. Plant counts were only accurate until growth stage 33, as after this stage, mainstems could not always be distinguished from tillers. Stems were counted as 'live' if their youngest leaf was green.

Sampling for dry weight and green area

The proportion of each sample used to estimate dry weight and photosynthetic area, varied according to growth stage. In S81, the whole sample was used for dry weight and green area until GS15 (end of January). After this, three plants of modal growth stage (about 10 per cent of the whole sample), were chosen to record photosynthetic areas. In S82, the whole sample was used for growth analysis until GS16 (end of March), followed by a one-third subsample until GS31 (end April). After this, at least 10 per cent by weight of the whole sample was used (with a minimum of 20 g fresh weight).

The plant material was divided into: (1) the non-green basal portion (or 'crown'), (2) the green leaf blade, (3) the green stem with leaf sheath, (4) non-green stem with leaf sheath, (5) ears (if more than 50 per cent emerged from the sheath), (6) dead plant material. The latter category included parts of leaves or tillers which had turned yellow, yet were still attached to the live plant.

No account was made of dead plants or detached plant parts (ie 'turnover'). The stem was always measured with its surrounding leaf sheath, and all references to stem weight refer to stem with leaf sheath.

The photosynthetic area of the plant was assumed to be the exposed green area. This was measured with a photo-electric leaf area meter, (LI - Cor Model LI 3000 Portable Area Meter[1]). Throughout the study, the following terminology is used: the green area index (GAI) is the total green area of the crop per unit ground surface; the leaf area index (LAI) is the green lamina area of the crop per unit ground surface; the ear area index is the green area of the ear minus the awns, per unit ground surface; the ear plus awn area index is the green ear with green awns area, per unit of ground surface.

The area of the lamina was taken by convention to be the area of one side of the leaf. For consistency with this measure, and in the absence of accurate information on the comparative rates of photosynthesis of ear stem and leaf, the green area of all organs was taken as one-half of the total green area. The green area of stems was calculated from their projected area, assuming the stem to be cylindrical. Ears were measured separately from stems if they were more than 50 per cent emerged from the leaf sheath.

The required ear area (grain with rachis) was calculated using the formula

$$Ae = m\,Ap(1 + c)$$

where Ae = half the total ear area

Ap = measured projected area of the ears with awns

m = the proportion of the ear + awns projected area contributed by the grain + rachis

c = correction factor, relating the width of the projected side of the ear (w_1) to the width of the shorter side (w_2)

$$c = w_2/w_1$$

This varied for variety and stage of grain filling.

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[1] Lambda Instruments Corporation, Lincoln, Nebraska.

The value of 'm' (the proportion of Ap contributed by the grain + rachis) was calculated as follows. Fifty ears were passed through the leaf area meter, first as complete ears with awns, and then as separate ears and awns. The projected area of the grain and rachis without awns contributed: 0.57 (±0.079) for two-row ears, 0.48 (±0.073) for six-row ears of the total projected area of ears with awns.

Since awns are almost flat, with only a small raised midrib, the required awns area was calculated using the formula:

$$Aa = Ap\ n/k$$

where Aa = ½ total awn area

Ap = measured projected area of the ear with awns

n = proportion of the measured projected area of the ear with awns contributed by the awns

k = proportion of the total projected awn area, actually measured when the awns are still attached to the ear

For two-row varieties n/k = 0.64 and for six-row varieties n/k = 0.74. These arbitrary ear (minus awn) and awn areas were corrected for the estimated percentage loss of chlorophyll from the ears and awns.

In S82, the length and width of the last four leaves was measured on plants used for dissection.

Following measurement for green area, all samples were dried in a 'Unitherm' forced draught oven at 90°C, and then weighed.

In S81, only the total dry weight of the shoots was measured until growth stage 31. After GS31, each subsample was separated into leaves and stem with leaf sheath. After anthesis the whole sample was separated into ears and straw, and the subsample ears divided into: awns with rachis, and grain.

In S82, dry weights were determined, where appropriate, for: non-green basal portion (crown); green leaf; stem with leaf sheath; dead leaves and tillers; grain; and awns with rachis. The whole sample was separated into ears and straw after ear emergence.

Five sample areas per replicate, of 500 mm x 2 rows, were taken each year for the final harvest at mean growth stage 92 (3 August 1981, 4 August 1982). In the laboratory the roots were cut off and loose soil shaken from the straw. Ears were cut from the stems, counted and weighed, then threshed in a small hand-fed threshing machine. Records were made of ear dry weight, grain dry weight, chaff dry weight and 1000 grain weight for each sample. The straw was weighed, dried then reweighed. In S82, the following information was also obtained: the number of grains per ear on 30 ears per replicate; the number and dry weight of median and lateral grains on five ears chosen at random from each six-row plot; and the individual grain weight of all grains on one ear chosen at random from each six-row variety plot.

Plant development

In S81, three plants of modal growth stage were chosen from each replicate at each harvest. In S82, either one (September to March) or two (March to August) plants per replicate were used. The mainstems of these plants (and, in S81, the tiller in the axil of the first leaf, the T1 tiller) were dissected under a stereo microscope. The number of leaves and live spikelet primordia, and the development stage of the apex were recorded (Kirby & Appleyard, 1981b).

Using a graduated microscope eye piece the dimensions of the developing ear were recorded, and its volume calculated in S82. Between collar initiation and apex tip death the shape of the developing ear was best described as shown in Figure 2.2.2a. After tip death the ear became more cuboid in shape (Fig. 2.2.2b).

Mainstem ear fresh weight was recorded after growth stage 31 in S82. After anthesis the number of grains and infertile florets were noted. Emerged ears were separated into grain, and awns with rachis, to be dried and weighed separately.

Carbohydrate analysis

On three dates in 1982 (4 February, 9 March, 29 April) the water soluble carbohydrate (WSC) content of plants was measured in order to

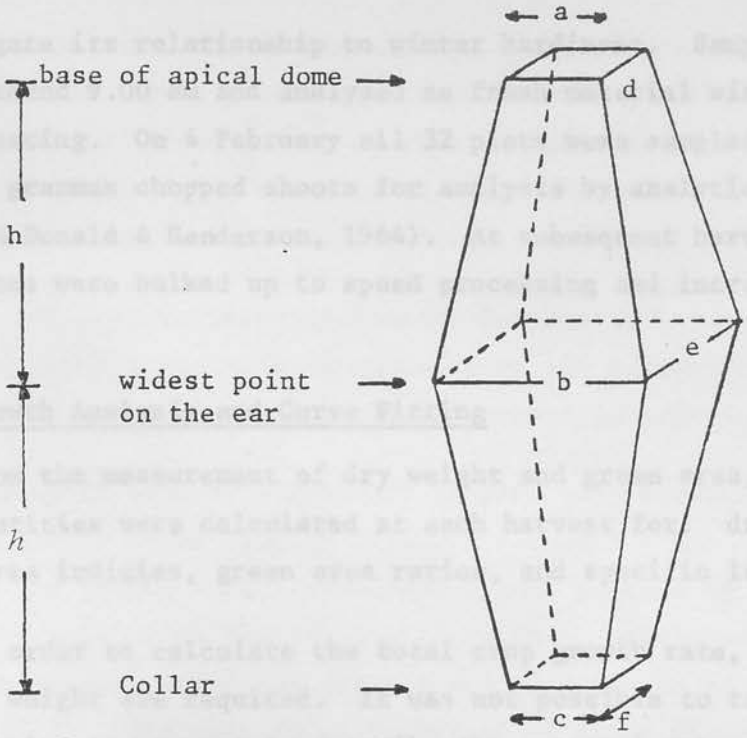

Fig 2.2.2 a Ear volume before tip death.

$$\text{Ear volume} = \left\{\left(\frac{be}{3} \times \frac{hb}{b-a}\right) - \left[\frac{ad}{3} \times h\left(\frac{b}{b-a} - 1\right)\right]\right\} + \left\{\left(\frac{be}{3} \times \frac{hb}{b-c}\right) - \left[\frac{cf}{3} \times h\left(\frac{b}{b-c} - 1\right)\right]\right\}$$

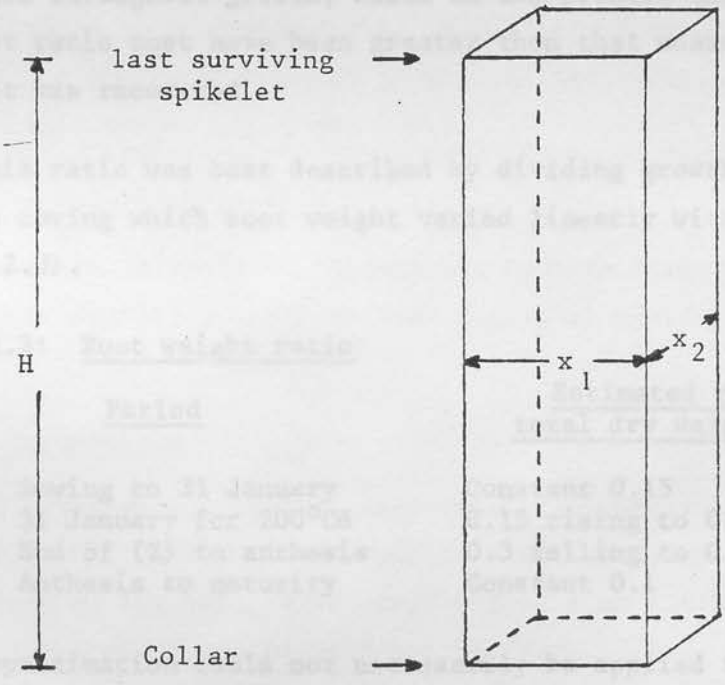

Fig 2.2.2 b Ear volume after tip death
x_1 = mean ear width, x_2 = mean ear breadth
Ear volume = $x_1 x_2 H$

investigate its relationship to winter hardiness. Samples were taken around 9.00 am and analysed as fresh material within two hours of harvesting. On 4 February all 32 plots were sampled separately to give 25 grammes chopped shoots for analysis by analytical laboratory staff (McDonald & Henderson, 1964). At subsequent harvests two replicates were bulked up to speed processing and increase the sample size.

2.3 Growth Analysis and Curve Fitting

From the measurement of dry weight and green area, growth analysis quantities were calculated at each harvest for: dry weight ratios, green area indicies, green area ratios, and specific leaf area.

In order to calculate the total crop growth rate, measurements of root weight are required. It was not possible to take sufficient root samples to accurately describe the seasonal pattern of root growth. There were no consistent differences between treatments in the root to shoot ratio throughout the period of measurement. Using published data for root to shoot ratio in cereals (Fukai, Koh & Kamura, 1976; Gallagher & Biscoe, 1978; Gregory *et al.*, 1978; Welbank *et al.*, 1974) and the measurements of root weight, the root to total dry weight ratio was estimated throughout growth, based on the premise that the true root to shoot ratio must have been greater than that measured since not all the root was recovered.

This ratio was best described by dividing growth into four periods during which root weight varied linearly with shoot weight (Table 2.3).

TABLE 2.3: Root weight ratio

	Period	Estimated root to total dry weight ratio
1.	Sowing to 31 January	Constant 0.15
2.	31 January for 200°Cd	0.15 rising to 0.3 at 200°Cd
3.	End of (2) to anthesis	0.3 falling to 0.1
4.	Anthesis to maturity	Constant 0.1

This approximation could not necessarily be applied to other crops, particularly in periods (1) and (2) as these depend upon a short cool autumn period followed by a cold winter allowing little or no growth. The rise in root weight ratio from 0.15, occurred as

temperatures increased in the spring. This rise could occur before winter if the autumn period were warm or sowing early (Fukai, Koh & Kamura, 1976). Minor errors in this estimate are not important since even at a ratio of 0.3 an error of ± 0.1 (ie 0.2 to 0.4) gives only a 12.5 per cent variation in total weight.

The GENSTAT computer program of Rothamsted Experimental Station was used for the analysis of variance of all parameters at each harvest and for regression analysis where appropriate.

The small size of individual samples gave erratic variation in mean growth rates between adjacent harvests. The 'functional' approach to growth analysis overcomes this problem by fitting mathematical functions to the original data which smooth small deviations from the overall trend and enables growth rates to be calculated (Hunt, 1978). The most suitable method of curve fitting for the long series of data obtained, was to fit splined cubic polynomials which meet in 'knots' where adjacent curves agree in position, slope and rate of change of slope. The computer program of Parsons and Hunt (1981) was used for this purpose. This program fits curves to the natural logarithms of the primary data for dry weight and green areas, from which relative growth rates, leaf area ratios and unit leaf rates are derived. A full statistical apparatus is included in the program which gives confidence limits for all the interpolated points along the curve.

2.4 Meteorological Records

Standard daily 09.00 GMT weather records were available from the meteorological station at Bush House, alongside the S81 trial plots.

2.4.1 Temperature

In graminaceous plants, temperature is perceived at the stem apex (Peacock, 1975). The temperature of the apical meristem is determined by the soil temperature before stem extension, and later by air temperature at the apex height (Hay, 1978). However, for periods of a week or more, estimates of mean air temperature are close to apical temperatures in the British climate (Gallagher, 1976).

Mean air temperature was estimated from the average of daily maximum and minimum temperatures. Accumulated temperature or 'thermal time' (^{o}C days) (Baker, Gallagher & Monteith, 1980) was calculated from mean daily air temperatures. The base temperature chosen was 0^{o}C since growth of temperate cereals continues down to this temperature. Various base temperatures have been used by other workers and it may be that the base temperature varies with ontogeny or the response being measured (Nuttonson, 1957; Smith, 1967; Monteith, 1981; Angus *et al.*, 1981a; Kirby, Appleyard & Fellows, 1982). However, the response to temperature near to the base can be non-linear (Kemp & Blacklow, 1982) and other factors such as day length can affect plant responses, making the determination of a true base temperature impossible. Throughout this study, thermal time was calculated using the 'Agromet method' (Anon, 1969), with a base temperature of 0^{o}C, unless stated otherwise.

2.4.2 Solar radiation

Total solar radiation was not recorded at the meteorological station. However, the duration of bright sunshine was recorded, as estimated using a 'Campbell-Stopes' recorder, which burns a trace on paper whenever irradiance exceeds about 200 Wm^{-2} (Monteith, 1973).

Cowley's (1978) method was used to estimate total daily solar radiation from the hours of bright sunshine, using the expression:

$$G = G_o \quad \delta\left[a+b\left(n/_N\right)\right] + (1-d)\ a'$$

where
- G = the global solar irradiation
- Go = global irradiation above the atmosphere based on a solar constant of 1353 Wm^{-2}
- n = the duration of bright sunshine
- N = the maximum possible duration of sunshine, ie astronomical day length
- a,b are constants
- δ = 0 if n = 0
- δ = 1 if n = >0
- a' = the average value of G/Go for sunless days

The photosynthetically active radiation (PAR) was assumed to be 50 per cent of the total (diffuse and direct) solar radiation (Szeicz, 1974).

The fraction of the PAR actually available for photosynthesis (the absorbed PAR) was estimated using the method of Gallagher and Biscoe (1978):

$$Fp = 1-\exp(-0.9\ k\ \overline{L}\ )/1.10$$

where Fp = the absorbed fraction of PAR

$\overline{L}$ = the mean leaf area index

and k = an extinction coefficient equal to 0.44 for barley (Monteith, 1973)

The absorbed radiation (Fp) was assumed to be zero when the crop was covered with snow.

2.4.3 Weather during the experimental period

A summary of the weather during the growth of the crops, and the deviations from the 12-year average (1970-82) is shown in Table 2.4.3a and Figures 2.4.3a and b.

For S81, the weather differed from the long-term average principally in the low level of insolation in the autumn and summer. The persistently slightly lower temperatures in spring and summer led to a lower than average accumulated temperature in this period (Fig. 2.4.3b).

For S82, October's temperature was 3.6°C below the long-term average and the rainfall exceptionally high. This was followed by a very cold December (5.3°C below average) and a cold wet January. June 1982 was exceptionally wet with a low level of insolation. The soil moisture deficit (SMD), calculated by Penman's method (MAFF, 1976) and adjusted for winter barley by using MORECS data for the appropriate square, did not appear to seriously limit growth in either season.

TABLE 2.4.3a: Weather during the experimental period

Month	Air Temperature °C				Solar Radiation MJ m^{-2} day^{-1}				Rainfall (mm)				SMD on last day of month			
	1980/81		1981/82		1980/81		1981/82		1980/81		1981/82		1980/81		1981/82	
	Mean	DFA	Mean	DFA	Mean daily total	DFA	Mean daily total	DFA	Total	DFA	Total	DFA	Deficit (mm)	DFA	Deficit (mm)	DFA
SEP	12.6	+ 0.2	12.3	- 0.1	6.7	- 2.3	8.8	- 0.2	53	- 25	117	+ 39	-	-	-	-
OCT	7.4	- 1.8	5.6	- 3.6	4.8	- 0.5	5.8	+ 0.5	100	+ 9	169	+ 78	-	-	-	-
NOV	5.3	- 0.2	6.0	+ 0.5	2.2	- 0.6	2.6	- 0.2	134	+ 37	93	- 4	-	-	-	-
DEC	4.7	+ 0.9	-1.5	- 5.3	1.2	- 0.2	1.2	- 0.2	105	+ 23	47	- 35	-	-	-	-
JAN	3.5	+ 0.9	0.9	- 1.7	1.7	- 0.1	1.6	- 0.2	36	- 46	165	+ 83	-	-	-	-
FEB	2.4	- 0.4	4.1	+ 1.3	4.5	+ 0.4	2.1	- 2.0	44	- 9	41	- 12	-	-	-	-
MAR	5.4	+ 1.0	4.7	+ 0.3	6.3	- 0.8	8.0	+ 0.9	98	+ 16	73	- 9	-	-	-	-
APR	6.0	- 0.7	7.8	+ 1.1	12.9	+ 0.9	12.4	+ 0.4	18	- 30	26	- 22	38	+ 33	29	+ 24
MAY	9.5	- 0.4	9.2	- 0.7	13.1	- 2.3	16.1	+ 0.7	46	- 6	64	+ 12	66	+ 21	55	+ 10
JUN	11.6	- 1.4	12.1	- 0.9	15.1	- 1.3	12.1	- 4.3	65	+ 2	136	+ 73	73	+ 11	0	- 62
JUL	13.4	- 1.4	14.5	- 0.3	14.1	- 1.5	16.3	+ 0.7	69	+ 7	45	- 17	55	+ 23	16	- 16
AUG	14.5	- 0.2	13.5	- 1.2	12.2	- 1.1	12.8	- 0.5	20	- 51	62	- 9	57	+ 41	0	- 16

DFA - Deviation from average of 1970-82

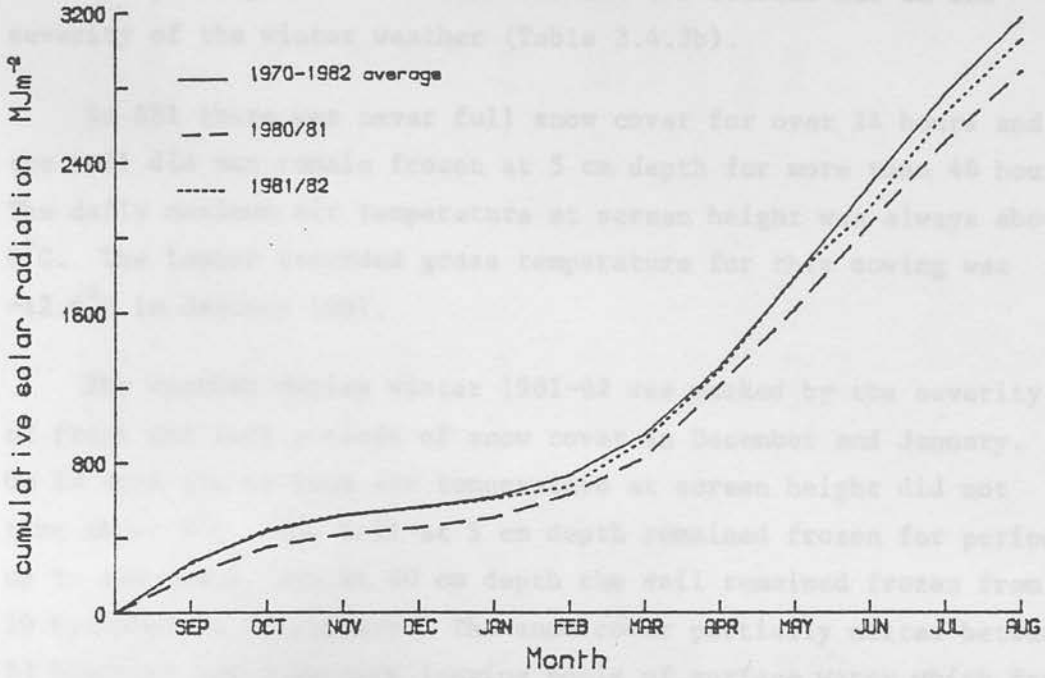

Fig. 2.4.3 a Solar radiation during the trials.
Calculated from monthly total sunshine hours using Cowley's (1978) method.

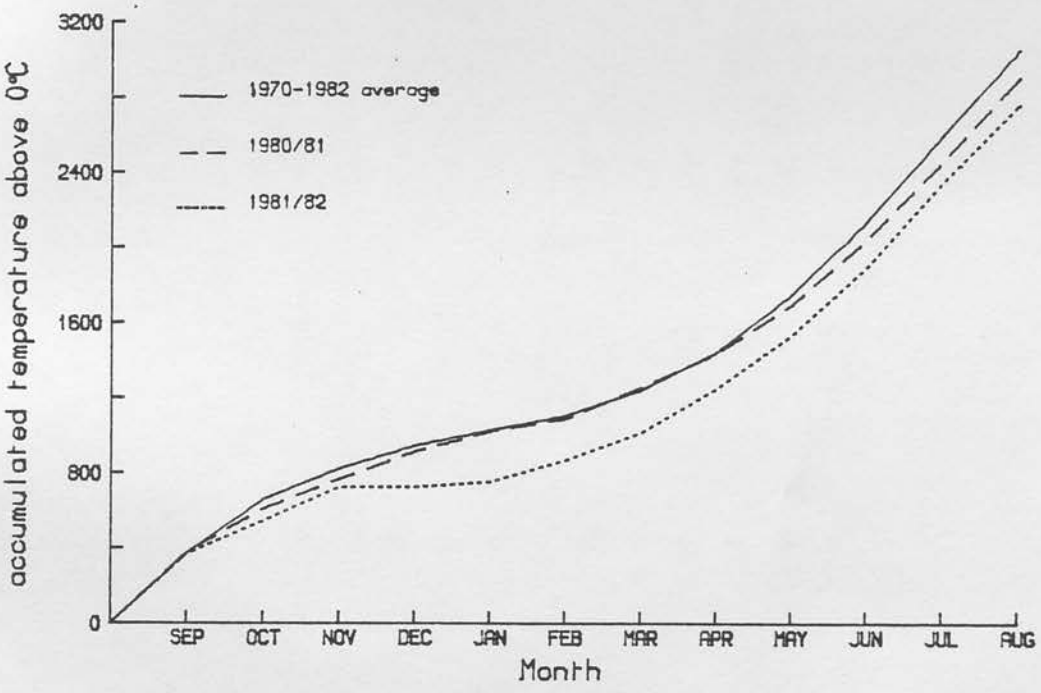

Fig. 2.4.3 b Accumulated temperature during the trials.
Calculated from mean monthly temperature using the simple remainder method.

The primary difference between the two seasons was in the severity of the winter weather (Table 2.4.3b).

In S81 there was never full snow cover for over 24 hours and the soil did not remain frozen at 5 cm depth for more than 48 hours. The daily maximum air temperature at screen height was always above $0^{o}C$. The lowest recorded grass temperature for this sowing was $-12.6^{o}C$ in January 1981.

The weather during winter 1981-82 was marked by the severity of frost and long periods of snow cover in December and January. On 12 days the maximum air temperature at screen height did not rise above $0^{o}C$. The soil at 5 cm depth remained frozen for periods up to two weeks, and at 20 cm depth the soil remained frozen from 10 December to 17 January. The snow cover partially melted between 23 December and 3 January leaving pools of surface water which froze around the plants in January. The lowest recorded grass temperature was $-25.5^{o}C$ in January 1982.

TABLE 2.4.3b: Severity of winter weather

		Days of full snow cover	Days soil frozen at 09.00 GMT			Days of Grass Frost	Lowest Grass Temperature °C	Lowest Air Temperature °C
			5 cm	10 cm	20 cm			
1980	October	0	0	0	0	14	- 9.0	- 3.3
	November	0	4	0	0	20	- 11.5	- 4.1
	December	0	5	1	0	19	- 10.5	- 3.9
1981	January	0	8	3	0	22	- 12.6	- 5.3
	February	0	10	4	0	21	- 12.4	- 5.7
	March	0	0	0	0	19	- 11.9	- 2.4
1981	October	0	0	0	0	14	- 8.2	- 2.4
	November	0	1	0	0	14	- 6.9	- 3.0
	December	18	23	22	20	27	- 14.7	- 13.5
1982	January	12	11	15	8	19	- 25.5	- 19.4
	February	0	3	0	0	16	- 10.6	- 5.9
	March	0	0	0	0	22	- 7.3	- 3.1

CHAPTER III

EXPERIMENTAL RESULTS

3.1 Crop Development

3.1.1 Seedling emergence

In the S82 sowings, the six-row cultivars emerged later than the two-row cultivars, requiring 20 per cent more accumulated temperature. Since there was no assessment of 50 per cent emergence in S81, it was assumed that these crops emerged in the same thermal time as in S821, which had been sown into a comparable environment. The S822 sowing was slower to emerge than the S821 sowing in terms of thermal time using a base of 0°C. However, if a higher base temperature was adopted (3°C for two-row cultivars and 4°C for six-row cultivars) both sowings emerged at the same thermal time (Table 3.1.1).

TABLE 3.1.1: Time to seedling emergence

Variety	Calendar time (days after sowing)			Thermal time °Cd (base = 0°C)		
	S81[1]	S821	S822	S81[1]	S821	S822
Gerbel	-	13	31	-	121 (69)[2]	188 (68)[2]
Athene	10	13	31	121	121 (69)[2]	188 (68)[2]
M. Otter	8	10	26	100	100 (70)[3]	148 (72)[3]
Igri	-	10	26	-	100 (70)[3]	148 (72)[3]
Video	8	-	-	100	-	-

[1] Estimates only for S81

[2] Base temperature = 4°C

[3] Base temperature = 3°C

3.1.2 Crop growth stages

There were no major varietal differences in the pattern of crop development. However, in S82 both Athene and Maris Otter took longer to reach stem elongation (GS31) than the other varieties, and in S822 the development of Maris Otter was delayed by one or two weeks in the spring and summer.

A summary of both the morphological development and ear development of Athene in all sowings is shown in Figure 3.1.2a. There was a considerable difference between sowings in the timing of leaf unfolding and tiller emergence, but after GS31 the development of the three sowings was more synchronised until anthesis. The difference in crop maturity between S81 and S82 after anthesis was caused by the slower ripening of S81; many more lower order tillers survived in S81 than in S82. The early crop development of each sowing was synchronised in thermal time from sowing, but this correlation was lost after GS31 (Fig. 3.1.2b).

The pattern of ear development also differed greatly between sowings, particularly in the timing of floral initiation and the time taken to pass through the reproductive stages before tip death. Tip death occurred soon after the start of stem elongation. There was remarkable synchrony in the date of mainstem anthesis in all sowings.

3.1.3 Leaf production and appearance

There was no significant difference between varieties in the number of leaves on the mainstem (Table 3.1.3a). The mean number of leaves in S821 was significantly higher than in S822 ($P = 0.05$).

TABLE 3.1.3a: Number of leaves initiated

Variety	Mainstem			T1 tiller
	S81	S821	S822	S81
Gerbel	-	11.9	11.1	-
Athene	11.8	12.1	11.5	9.0
M. Otter	11.2	11.9	11.8	8.4
Igri	-	11.6	11.2	-
Video	12.0	-	-	8.9

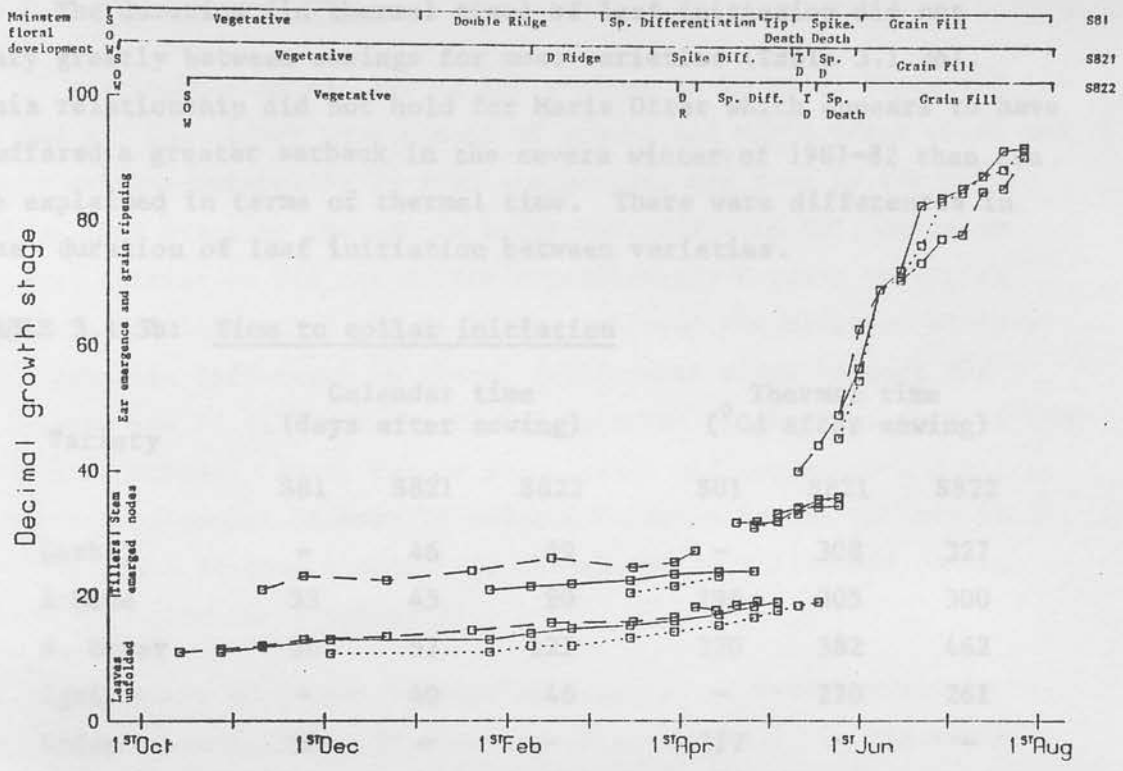

Fig. 3.1.2 a Crop development, calendar time.
Athene all sowings. — — S81 ——— S821 ------- S822

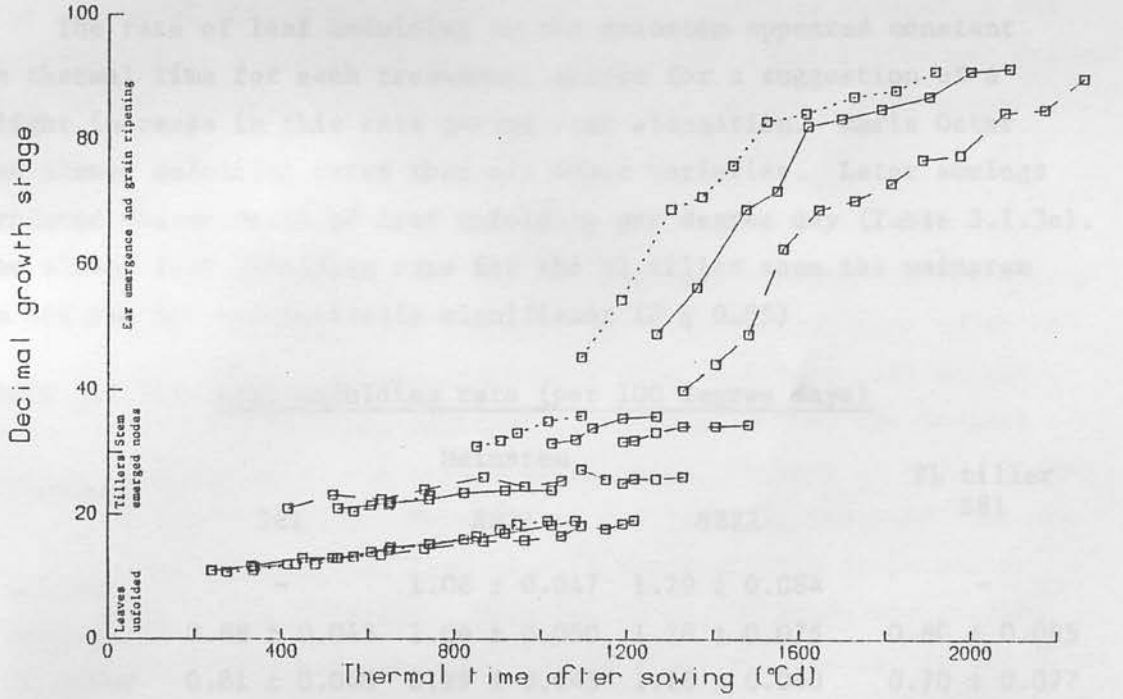

Fig. 3.1.2 b Crop development, thermal time. Athene all sowings.

The duration (in thermal time) of leaf initiation did not vary greatly between sowings for most varieties (Table 3.1.3b). This relationship did not hold for Maris Otter which appears to have suffered a greater setback in the severe winter of 1981-82 than can be explained in terms of thermal time. There were differences in the duration of leaf initiation between varieties.

TABLE 3.1.3b: Time to collar initiation

Variety	Calendar time (days after sowing)			Thermal time (°Cd after sowing)		
	S81	S821	S822	S81	S821	S822
Gerbel	-	46	99	-	308	327
Athene	33	45	90	296	305	300
M. Otter	36	57	123	320	382	462
Igri	-	40	46	-	270	261
Video	30	-	-	277	-	-

An accurate rate of leaf initiation could not be determined as leaf initiation ceased by the second or third harvest in all sowings.

The rate of leaf unfolding on the mainstem appeared constant in thermal time for each treatment, except for a suggestion of a slight increase in this rate during stem elongation. Maris Otter had slower unfolding rates than all other varieties. Later sowings produced faster rates of leaf unfolding per degree day (Table 3.1.3c). The slower leaf unfolding rate for the T1 tiller than the mainstem in S81 was not statistically significant ($P \leq 0.05$).

TABLE 3.1.3c: Leaf unfolding rate (per 100 degree days)

Variety	Mainstem			T1 tiller
	S81	S821	S822	S81
Gerbel	-	1.08 ± 0.047	1.29 ± 0.084	-
Athene	0.88 ± 0.043	1.06 ± 0.050	1.28 ± 0.075	0.80 ± 0.095
M. Otter	0.81 ± 0.040	0.99 ± 0.045	1.18 ± 0.060	0.70 ± 0.077
Igri	-	1.06 ± 0.048	1.29 ± 0.063	-
Video	0.91 ± 0.036	-	-	0.83 ± 0.097

Confidence limits at $P = 0.05$.

3.1.4 Floral Development

Development of the ear in S82 sowings is shown in Figures 3.1.4 a and b. The slower development of Athene and Maris Otter which was only evident externally by stem elongation, was seen at the double ridge (DR) stage on the ear in early February. In S81, mainstem floral initiation did not differ significantly between varieties and the development of the T1 tiller followed the mainstem closely. The greatest difference in floral development stage between the mainstem and T1 tiller was a 10 day interval at the triple mound (TM) stage in Athene. There was no significant difference ($P = 0.05$) in floral development between T1 and the mainstem in any variety in S81 at the start of stem elongation, though the T1 tiller did remain slightly later until maturity.

The start of floral initiation appeared to be dependant on accumulated temperature from sowing (Fig. 3.1.4b). In the variety Athene, the plants remained vegetative until about 450°Cd when the most advanced plants reached the DR stage; the whole crop reached this stage by 650°Cd. The DR stage of floral development was preceded by apical meristem elongation which marked the start of floral initiation; the timing of this event was not recorded. Meristem elongation was accompanied by a change in the rate of primordia initiation per degree day, which occurred between nine and 36 days before the DR stage (Table 3.1.4a). This change in initiation rate was evident in all treatments.

Floral development after the DR stage was reached did not appear to be solely dependant upon temperature. The thermal time spent at the DR stage varied between treatments (Fig. 3.1.2a). S81 Athene which achieved this stage earliest in the year waited the longest before progressing to the triple mound stage, whereas in S822, Athene showed no sign of delay. In general, the later in the year that the DR stage was reached, the less time it spent at this stage before progressing to the TM stage. Usually, if the DR stage was reached at any time before mid-February, the TM stage was reached in the first two weeks of March. When the DR stage was reached after mid-March the TM stage followed almost immediatiely (Table 3.1.4b). Table 3.1.4c shows the thermal time from the TM stage to the start of anthesis (the

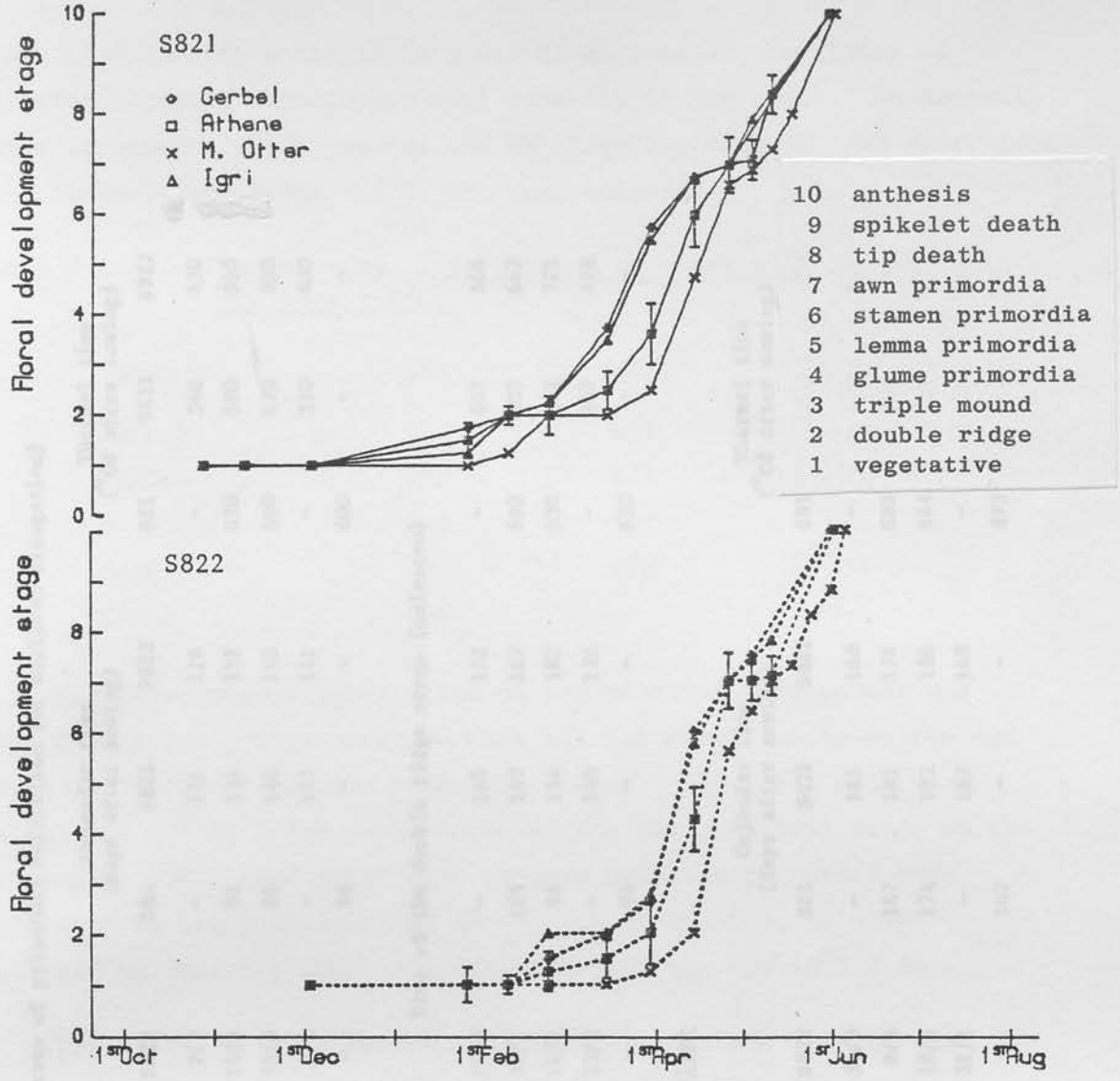

Fig 3.1.4 a Floral development, calendar time.

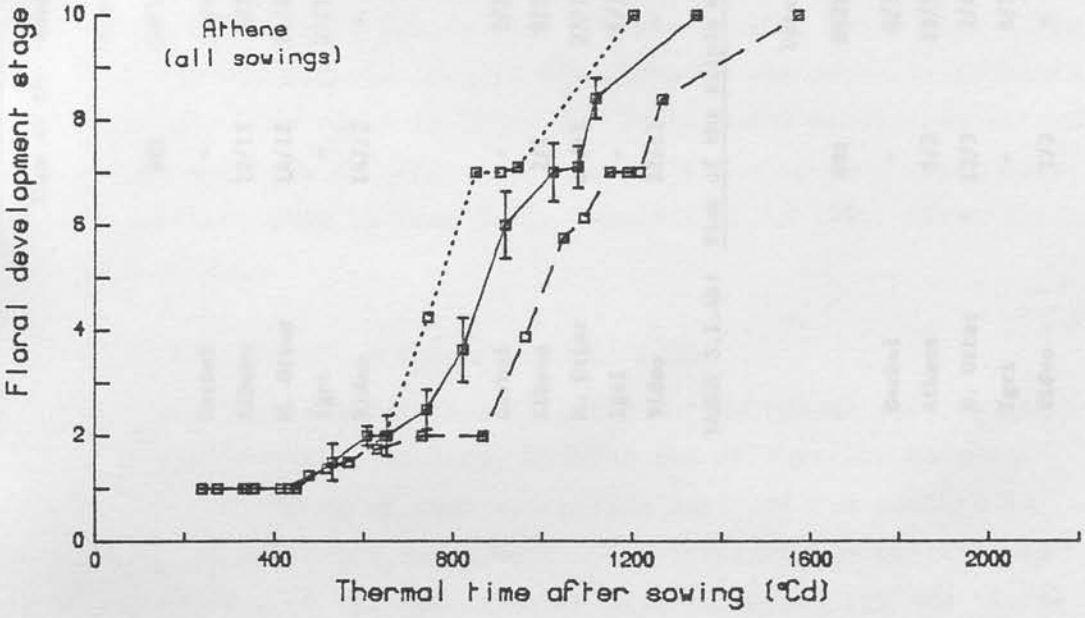

Fig 3.1.4 b Floral development, thermal time.

TABLE 3.1.4a: Floral initiation

Time of the change in rate of primordia initiation (at meristem elongation)

	Date			Calendar time (days after sowing)			Thermal time (^{o}Cd after sowing)		
	S81	S821	S822	S81	S821	S822	S81	S821	S822
Gerbel	-	31/1	7/2	-	131	116	-	560	430
Athene	20/12	3/2	14/3	92	134	151	620	580	560
M. Otter	14/12	11/2	22/3	86	142	160	600	620	600
Igri	-	23/1	2/2	-	123	111	-	510	400
Video	14/12	-	-	86	-	-	600	-	-

Time of the double ridge stage (mainstem)

Gerbel	-	9/2	15/3	-	140	152	-	607	566
Athene	2/1	9/2	30/3	105	140	167	690	607	647
M. Otter	22/12	23/2	14/4	94	154	182	630	652	775
Igri	-	9/2	23/2	-	140	132	-	607	478
Video	22/12	-	-	94	-	-	630	-	-

TABLE 3.1.4b: Time of the triple mound stage

	Date			Calendar time (days after sowing)			Thermal time (^{o}Cd after sowing)		
	S81	S821	S822	S81	S821	S822	S81	S821	S822
Gerbel	-	6/3	31/3	-	165	168	-	710	652
Athene	5/3	23/3	6/4	167	181	174	889	769	696
M. Otter	12/3	2/4	18/4	174	192	186	944	839	777
Igri	-	8/3	31/1	-	167	168	-	718	652
Video	1/3	-	-	162	-	-	879	-	-

start of whole crop anthesis is a better measure of the timing of mainstem anthesis than 50 per cent anthesis in the crop). In general, those treatments which reached the TM stage earliest in the year, took more thermal time (base = $0^{o}C$) to reach anthesis.

TABLE 3.1.4c: Thermal time, triple mound to start of anthesis (^{o}Cd base = $0^{o}C$)

Variety	S81	S821	S822
Gerbel	-	633	533
Athene	695	574	506
M. Otter	640	537	492
Igri	-	625	533
Video	628	-	-

The first morphological sign of reproductive development was stem elongation. This occurred when all the floral parts of the ear had been initiated (stamen primordia stage). The first node was detectable (GS31) a few days later at the awn primordia stage on the developing ear. Soon after GS31 no more spikelet primordia were initiated on the mainstem apex (or T1 tiller in S81); this was followed by apex tip death and spikelet abortion (Table 3.1.4d).

The possible influence of photoperiodic control between the attainment of the DR stage and GS31 is seen in the range of dates for these events. Attainment of the DR stage ranged from 22 December to 14 April whereas GS31 was reached between 6 April and 6 May. This range in dates was reduced to just nine days by the start of anthesis (Table 3.1.4e). The range in dates for 50 per cent whole crop anthesis was greater, due both to differences in tillering between treatments and a significant drop in mean daily temperature in 1982, after the first week of June.

3.1.5 Plant morphology and floral development

There was little difference in early morphological development between varieties within sowings, however the differences between varieties in the timing of stem elongation were evident earlier in floral initiation. Hence there were often considerable differences between treatments in the relationship between morphology and floral

TABLE 3.1.4d: Stem elongation (mainstem)

Time to the awn initial stage (days after sowing)

Variety	S81	S821	S822
Gerbel	-	215	193
Athene	207	215	193
M. Otter	207	226	209
Igri	-	215	193
Video	197	-	-

Time to first node detectable (GS31) (days after sowing)

Variety	S81	S821	S822
Gerbel	-	204	190
Athene	209	211	195
M. Otter	199	218	204
Igri	-	204	190
Video	201	-	-

Time to maximum spikelet number (days after sowing)

Variety	S81	S821	S822
Gerbel	-	216	194
Athene	213	224	202
M. Otter	217	224	216
Igri	-	216	202
Video	206	-	-

Time to apex tip death (days after sowing)

Variety	S81	S821	S822
Gerbel	-	222	206
Athene	226	230	213
M. Otter	231	236	220
Igri	-	226	211
Video	220	-	-

TABLE 3.1.4e: Anthesis

Variety	Date			Calendar time (days after sowing)			Thermal time (°Cd after sowing)		
	S81	S821	S822	S81	S821	S822	S81	S821	S822
				Time of the start of anthesis					
Gerbel	-	31/5	1/6	-	251	230	-	1343	1185
Athene	3/6	31/5	2/6	257	251	231	1584	1343	1202
M. Otter	3/6	2/6	6/6	257	253	235	1584	1376	1269
Igri	-	31/5	1/6	-	251	230	-	1343	1185
Video	28/5	-	-	251	-	-	1507	-	-
				Time of 50 per cent ear emergence					
Gerbel	-	31/5	2/6	-	251	231	-	1343	1202
Athene	1/6	1/6	4/6	255	252	233	1558	1359	1236
M. Otter	3/6	17/6	22/6	257	268	251	1584	1565	1440
Igri	-	31/5	4/6	-	251	233	-	1343	1236
Video	29/5	-	-	252	-	-	1517	-	-
				Time of 50 per cent anthesis					
Gerbel	-	2/6	1/6	-	253	232	-	1376	1219
Athene	4/6	2/6	5/6	258	253	234	1595	1376	1255
M. Otter	6/6	14/6	19/6	260	265	248	1619	1534	1411
Igri	-	2/6	5/6	-	253	234	-	1376	1255
Video	1/6	-	-	255	-	-	1559	-	-

development before GS31. This is demonstrated in Figure 3.1.5 which compares floral development with the number of leaves unfolded for the widest range of situations observed. In general, the S82 sowing attained a certain floral development stage with fewer leaves unfolded than the S81 or S821 sowings. There was little difference between varieties in S81 for this factor, but in S82 sowings Gerbel had fewer leaves, and Maris Otter more leaves at each floral stage, than other varieties. The range of disparity between internal and external development seemed to be greatest at the attainment of the double ridge stage. At this stage in the S822 sowing the four varieties: Igri, Gerbel, Athene and Maris Otter had 2, 3, 4 and 5 leaves unfolded, respectively. This was not a consistent varietal characteristic since Igri had four leaves unfolded when the DR stage was reached in S821.

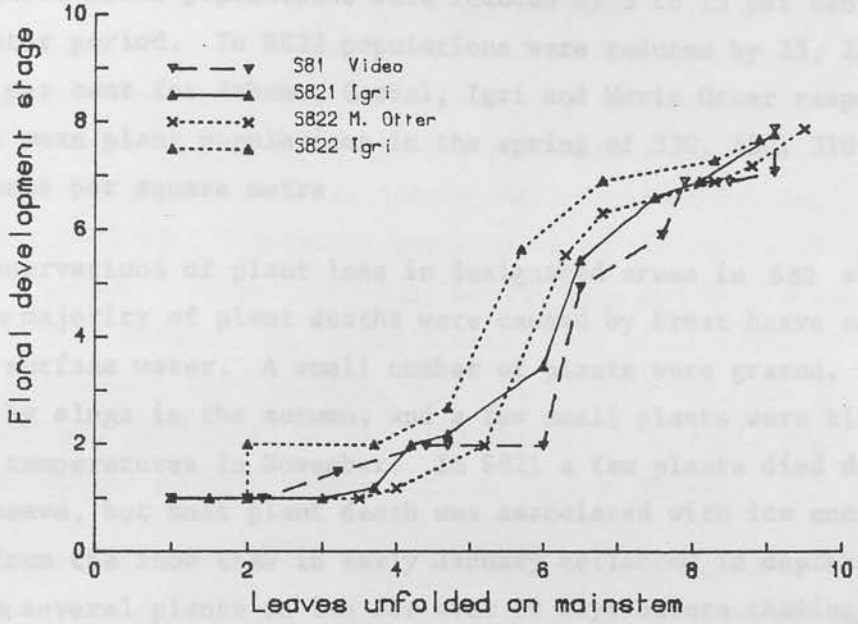

Fig. 3.1.5 The relation between plant morphology and floral development. Selected treatments to show the range of patterns observed.

3.2 Winter Survival

3.2.1 Plant death

There was no plant death due to frost damage in S81. In S821 the initial plant populations were reduced by 5 to 15 per cent in the winter period. In S822 populations were reduced by 23, 25, 28 and 38 per cent for Athene, Gerbel, Igri and Maris Otter respectively, to give mean plant populations in the spring of 330, 330, 310 and 280 plants per square metre.

Observations of plant loss in designated areas in S82 showed that the majority of plant deaths were caused by frost heave and frozen surface water. A small number of plants were grazed, and killed by slugs in the autumn; and a few small plants were killed by low temperatures in November. In S821 a few plants died due to frost heave, but most plant death was associated with ice encasement. Water from the snow thaw in early January collected in depressions, encasing several plants in ice for over 10 days before thawing. Maris Otter was very susceptible to ice encasement and Athene particularly hardy in these conditions. Plant death appeared to continue until the end of March; however, it is probable that shoots which had been separated from their roots due to frost heave in January, were not immediately evident, because low temperatures delayed leaf senescence.

3.2.2 Leaf scorch and stress

In S81 the first signs of leaf scorch were apparent by 6 November after four nights of ground frost (one at -11.5°C). Maris Otter had more scorch of basal leaf tips than Video or Athene. Signs of cold stress were noticed on 2 March as purpling of the leaves, following the longest cold spell of the winter with ground frosts generally at -10°C. Video exhibited deeper purpling than Maris Otter which had more than Athene.

In 1981-82 fuller records were kept of leaf damage and stress, though snow cover throughout most of the severe weather, prevented any recording in this period. Air temperatures first fell below 0°C on 13 October. All the S821 varieties with one leaf unfolded

showed purpling of the basal sheaths on 14 October but to a smaller degree in Athene than other cultivars. Purpling of the leaves was evident in both S82 sowings on 19 November after four nights of mild ground frost but not evident on 26 November after three nights of frost, as the plants had apparently hardened. There were no visible signs of plant stress at the end of the severe cold period on 20 January nor on 12 February. However, on 23 February after a period of night frosts the following situation was evident. S822 Igri - severe purpling of all leaves; S822 Maris Otter, S821 Maris Otter and S821 Igri - moderate purpling of all leaves; S821 Gerbel and S822 Gerbel - slight purpling; S821 Athene and S822 Athene - no signs of cold stress. On 22 March there were still signs of cold stress decreasing from moderate purpling in S822 Igri and S821 Maris Otter through S822 Maris Otter, S822 Gerbel, S821 Igri, S821 Gerbel, and S822 Athene to S821 Athene with no sign of stress.

Leaf scorch showed the same varietal differences as seen for cold stress symptoms, but since the oldest leaves scorched first the S821 sowing suffered the greatest leaf loss (death of the youngest leaf usually denotes apical death). The first leaf of all varieties in S821, except Athene, were scorched in November. There was no sign of leaf damage in S822 before the winter. During the severe cold and snow cover between 13 December and 20 January there was no change in morphological growth stage (S822 at GS11/20, S821 at 13/21 or 13/22) but there was some leaf scorch and death to give the situation shown in Table 3.2.2a.

After 20 January only Maris Otter suffered more leaf scorch; by 12 February Maris Otter had scorch on the fifth leaf in S821 and the third leaf in S822. There was no further scorch in any treatment by 23 February. The differences between treatments in cold stress and leaf scorch were reflected in the amount of harvested crop which was dead (Table 3.2.2.b). No records were kept of leaf scorch in S81.

TABLE 3.2.2a: Leaf death and scorch on 20 January 1982

	Dead Leaves				Remaining Leaves Scorched at Tip					
	All 1st leaves	Some 1st leaves	All 2nd leaves	Some 2nd leaves	All 1st leaves	Some 1st leaves	All 2nd leaves	Some 2nd leaves	All 3rd leaves	Some 3rd leaves
S821										
Gerbel	✓	✓	–	✓	–	–	✓	✓	–	✓
Athene	✓	✓	–	–	–	–	–	✓	–	✓
M. Otter	✓	✓	–	✓	–	–	✓	✓	–	✓
Igri	✓	✓	–	✓	–	–	✓	✓	–	✓
S822										
Gerbel	–	–	–	–	–	✓	–	✓	–	–
Athene	–	–	–	–	–	✓	–	✓	–	–
M. Otter	–	✓	–	–	✓	✓	–	✓	–	–
Igri	–	–	–	–	–	✓	–	✓	–	–

TABLE 3.2.2b: Dead portion to shoot dry weight ratio

	Harvest 26 January	Harvest 9 February
S821		
Gerbel	0.14	0.07
Athene	0.11	0.08
M. Otter	0.15	0.10
Igri	0.12	0.09
S822		
Gerbel	0.04	0.06
Athene	0.05	0.04
M. Otter	0.11	0.20
Igri	0.06	0.08
s.e. of mean (21 d.f.)	0.036	0.032
L.S.D. for treatment means ($P = 0.05$)	0.052	0.046

3.2.2 Carbobydrate analysis

The three harvests on 4 February, 9 March and 29 April 1982 gave mean water soluble carbohydrate (WSC) content in the dry matter of 5, 13 and 17 per cent, respectively. There was no significant difference between sowings in the WSC content at each harvest ($P \leq 0.05$). The main varietal difference was that S822 Maris Otter had a significantly lower WSC content than other treatments at each sampling time.

In order to examine the relationship between the WSC content and frost hardiness, the dead portion to shoot weight ratio at adjacent dry weight harvests was regressed against the WSC content. Using the dead weight ratio, though a better measure of frost hardiness than plant death, had limitations since it was affected by both the rate of growth and the rate of tissue death. This ratio also had high standard errors (see Table 3.2.2b). In order to distinguish between varietal differences in WSC content and differences due to plant size, the mean dry weight per plant at adjacent harvests was also regressed against the WSC content.

The actual proportion of dead plant tissue in the samples used for WSC analysis was not measured, but a large dead portion would have lowered the percentage WSC content in the sample dry matter. To assess the maximum effect this would have on the percentage WSC content, a correction was applied to account for the dead weight ratio at the adjacent dry weight harvest, thus converting the WSC figure to a 'live plant' basis.

On 4 February there was a significant correlation between the WSC content in the dry matter and the dead weight ratio (Fig. 3.2.3a). The equation of the fitted line was

$$y = 0.34\ (\pm\ 0.049) - 0.0525\ (\pm\ 0.0103)\ x$$

and accounted for 84 per cent of the variance (r = 0.93, d.f. = 7), using the mean dead weight ratio from harvests nine days before and five days after the WSC test. When the correction for WSC content in the 'live plant' was applied, the regression accounted for 70 per cent of the variance: $y = 0.41\ (\pm\ 0.088) - 0.060\ (\pm\ 0.017)\ x$, ($r$ = 0.86, d.f. = 7).

The nearest dry weight sample harvests to the WSC test on 9 March were 23 February and 15 March. The regression of dead weight ratio on WSC content was only significant if just the latter harvest was included, and accounted for 78 per cent of the variance or 71 per cent using adjusted WSC content in the 'live plant'. However, this relationship was based primarily upon the position of S822 Maris Otter (Fig. 3.2.3a).

On 29 April there was no longer any relationship between the WSC content and the dead weight ratio. There was however, a good correlation with mean individual plant dry weight (Fig. 3.2.3b) accounting for 61 and 66 per cent of the variance for WSC content in the dry matter and WSC content in 'live plant' dry matter respectively (r = 0.82, r = 0.84, d.f. = 7). The order of plant dry weight at this harvest was a good indicator of the relative growth stage of the crops. All treatments had started stem elongation and the number of nodes detectable ranged from 0.3 in S822 Maris Otter to 3.0 in S821 Igri.

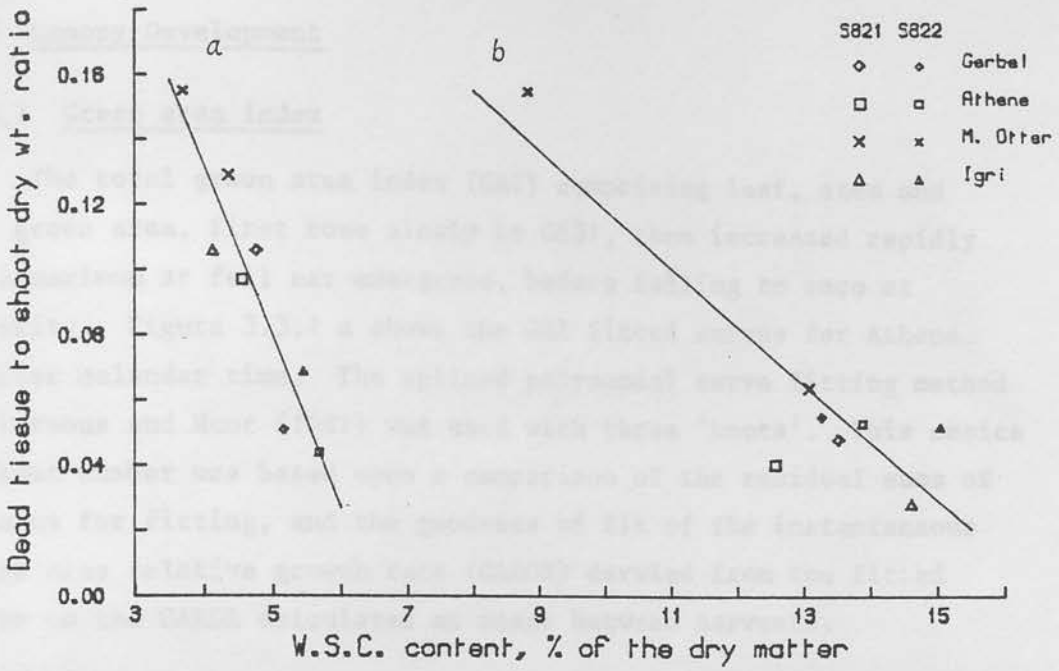

Fig 3.2.3 a The relation between the water soluble carbohydrate content and leaf senescence. *a* :- WSC on 4 Feb. '82, dead wt. ratio mean of 26 Jan. '82 and 9 Feb. '82. Fitted line y = 0.34 - 0.053x. *b* - WSC on 9 March '82, dead weight ratio on 15 March '82, fitted line y = 0.30 - 0.18x.

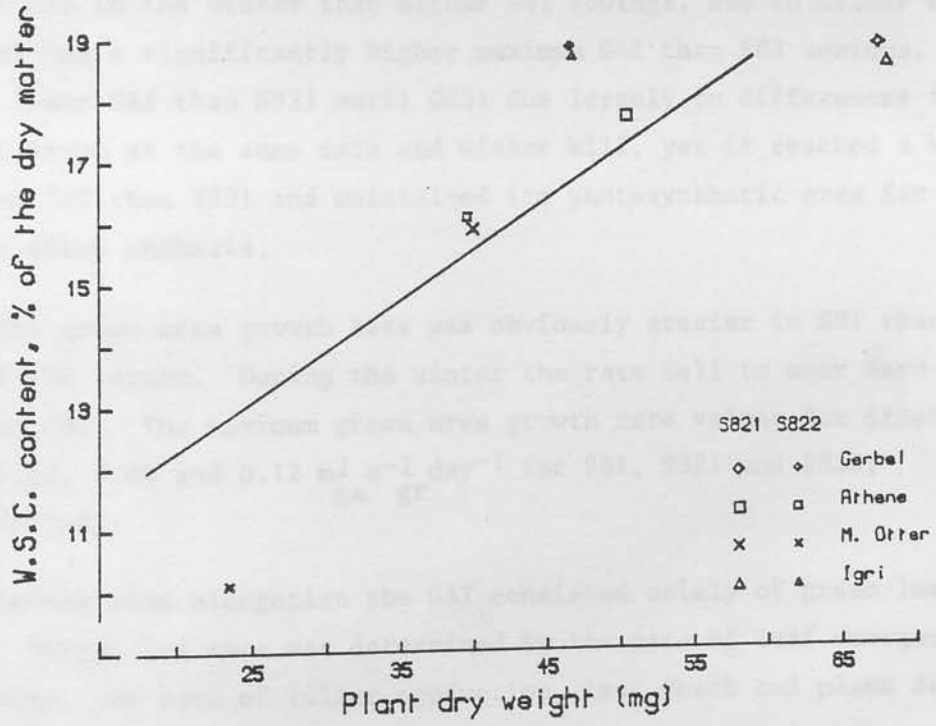

Fig 3.2.3 b The relation between the water soluble carbohydrate content on 29 April '82 and plant dry weight mean of 26 April '82 and 4 May '82. Fitted line y = 9 + 0.17x.

3.3 Canopy Development

3.3.1 Green area index

The total green area index (GAI) comprising leaf, stem and ear green area, first rose slowly to GS31, then increased rapidly to a maximum at full ear emergence, before falling to zero at maturity. Figure 3.3.1 a shows the GAI fitted curves for Athene against calendar time. The splined polynomial curve fitting method of Parsons and Hunt (1981) was used with three 'knots'. This choice of knot number was based upon a comparison of the residual sums of squares for fitting, and the goodness of fit of the instantaneous green area relative growth rate (GARGR) dervied from the fitted curve to the GARGR calculated as means between harvests.

Within each sowing there was rarely any significant difference in GAI between varieties at a comparable growth stage. In S81, Athene had a lower GAI than Maris Otter or Video up to GS31. In S821, Maris Otter had a significantly lower maximum GAI than the other varieties.

Differences between sowings were greater. S81 had a significantly higher GAI in the winter than either S82 sowings, due to milder weather; it also had a significantly higher maximum GAI than S82 sowings. S822 had a lower GAI than S821 until GS31 due largely to differences in growth stage at the same date and winter kill, yet it reached a higher maximum GAI than S821 and maintained its photosynthetic area for longer after anthesis.

The green area growth rate was obviously greater in S81 than S82 in the autumn. During the winter the rate fell to near zero at maximum GAI. The maximum green area growth rate values for Athene were 0.12, 0.06 and 0.12 $m^2_{ga}\ m^{-2}\ day^{-1}_{gr}$ for S81, S821 and S822, respectively.

Before stem elongation the GAI consisted solely of green leaf area. Hence, its rate was determined by the rate of leaf emergence, leaf size, the rate of tiller production, leaf death and plant death.

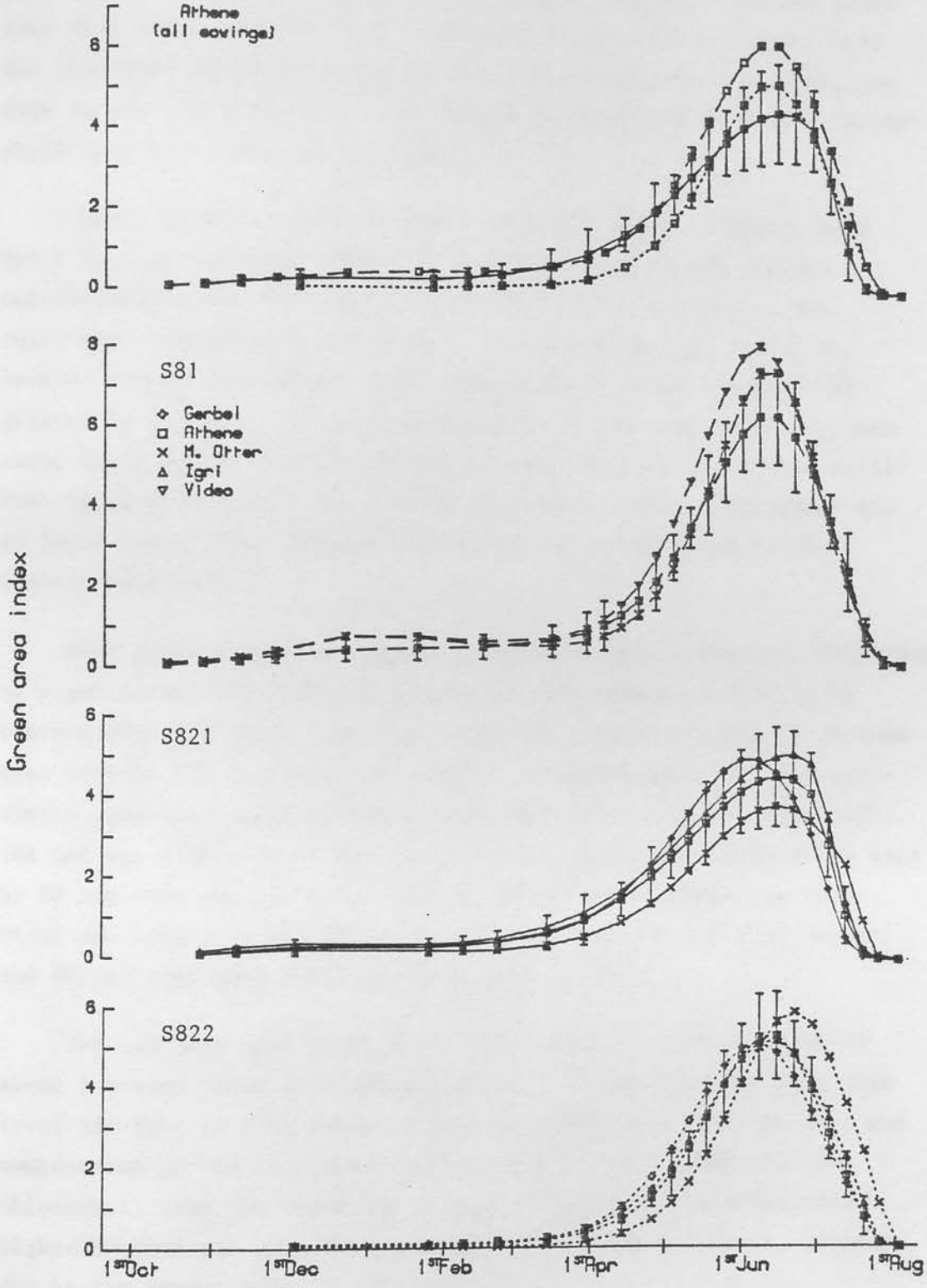

Fig 3.3.1 a Seasonal change in the green area index.
Fitted curves showing 95% confidence limits for Athene.

Between GS31 and maturity, first stem green area, and then ear green area were added to leaf area. Expansion of the photosynthetic area was then also affected by the rate of stem extension, stem size, the rate of ear emergence, ear + awn size,tiller death, and loss of chlorophyll from the stem, ear and awns.

Lamina area reached a maximum a few days before anthesis when the flag leaf unfolded. Most of the differences in GAI between cultivars were due to differences in leaf area index (LAI), but there was no significant difference in the maximum LAI (about 3) between sowing date means. Leaf area duration after anthesis was greater in S81 than S82 as it maintained its LAI near to its maximum value for a longer period. After anthesis, the LAI of six-row cultivars decreased sooner than that of the two-row types, presumably due to fewer lower order tillers lagging behind the mainstem in the six-row cultivars.

Stem green area also reached a maximum around anthesis. There was no significant difference in stem green area between varieties or between S821 and S822. However, there was a great difference in stem area between S81 and S82; for example, at maximum GAI, all photosynthetic area components of Maris Otter were greater in S81 than S821, the GAI was higher by 54 per cent, LAI by 25 per cent, stem green area by 89 per cent and ear green area by 59 per cent. Comparing Maris Otter and Athene in S81 with S82, mainstems were 20 per cent longer, and 40 per cent more stems produced ears, in S81.

The ear plus awns green area index reached a maximum value of about 1.0 soon after full ear emergence. It then remained near this level for four to five weeks as loss of chlorophyll from the awns was compensated by the increasing size of grains until these too lost chlorophyll from the lemma and palea. Athene had a significantly higher maximum ear plus awn area index than other cultivars, largely due to its larger awns.

The rates of leaf tiller and ear emergence, and stem elongation were all temperature dependent, hence the rate of increase of GAI was also related to temperature. Plotting recorded GAI up to its maximum value, against accumulated temperature from sowing (Fig. 3.3.1b

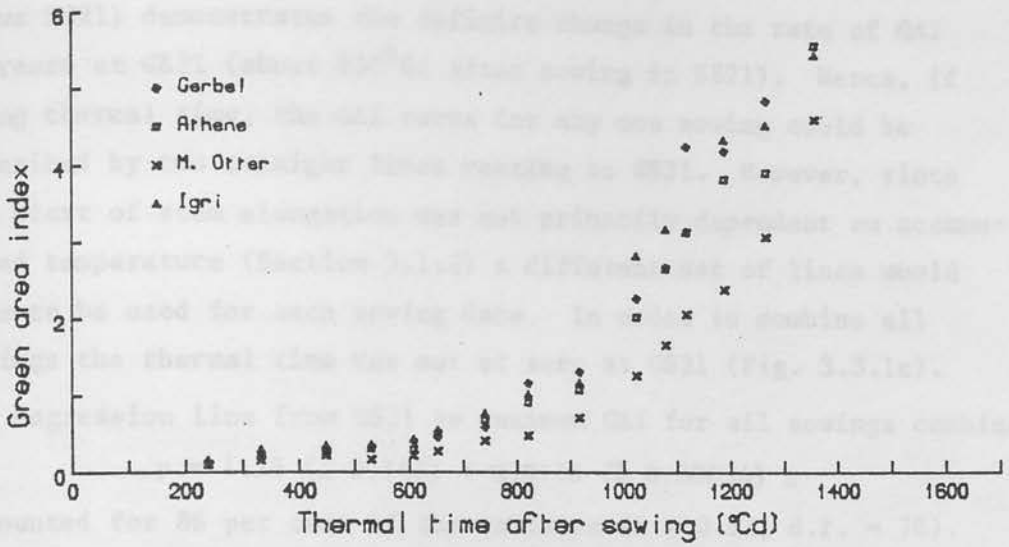

Fig. 3.3.1 b The increase in GAI in S821 with thermal time.

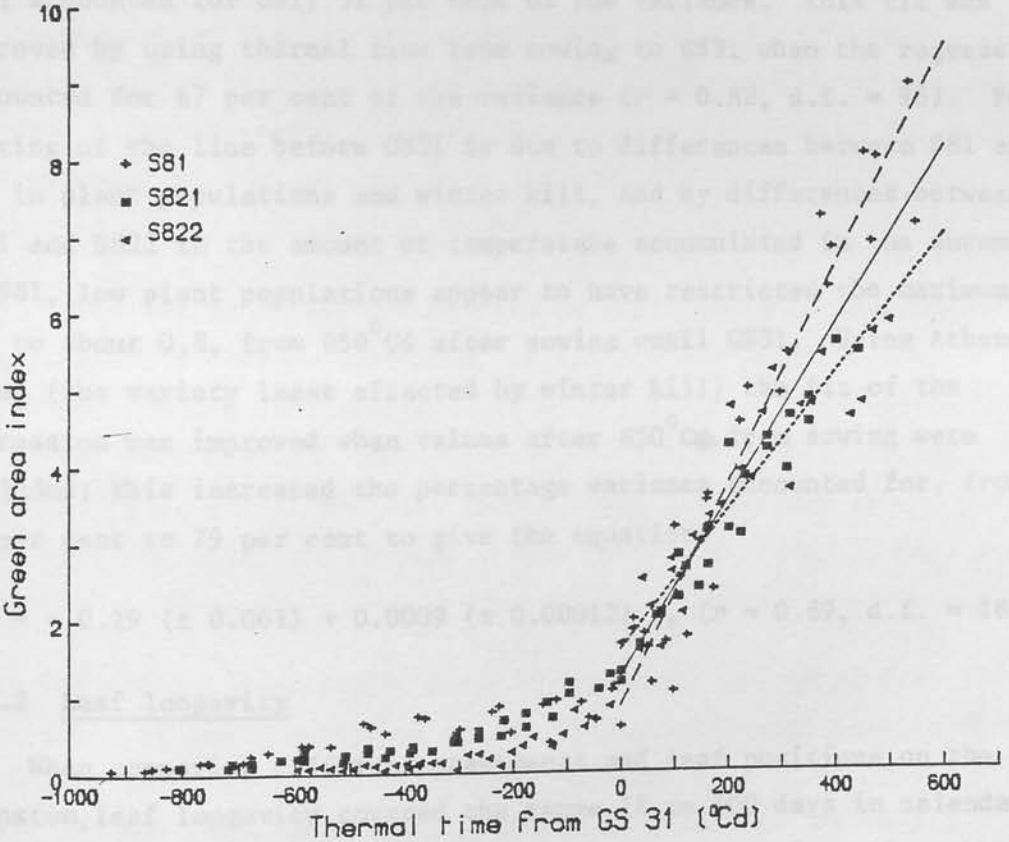

Fig. 3.3.1 c The increase in GAI with thermal time.
Fitted lines: —— mean of all sowings, y = 1.25 + 0.0116x:
– – S81, y = 0.86 + 0.0145x; ----- S82, y = 1.61 + 0.0091x.

shows S821) demonstrates the definite change in the rate of GAI increase at GS31 (about 950°Cd after sowing in S821). Hence, if using thermal time, the GAI curve for any one sowing could be described by two straight lines meeting at GS31. However, since the start of stem elongation was not primarily dependent on accumulated temperature (Section 3.1.2) a different set of lines would have to be used for each sowing date. In order to combine all sowings the thermal time was set at zero at GS31 (Fig. 3.3.1c). The regression line from GS31 to maximum GAI for all sowings combined:

$$y = 1.25\ (\pm\ 0.141) + 0.0116\ (\pm\ 0.00054)\ x$$

accounted for 86 per cent of the variance (r = 0.92, d.f. = 76). Both the rate of increase after GS31 and the duration of increase in GAI were greater in S81 than in S82.

Fitting a regression line to accumulated temperature before GS31 accounted for only 52 per cent of the variance. This fit was improved by using thermal time from sowing to GS31 when the regression accounted for 67 per cent of the variance (r = 0.82, d.f. = 96). Poor fitting of the line before GS31 is due to differences between S81 and S82 in plant populations and winter kill, and by differences between S821 and S822 in the amount of temperature accumulated in the autumn. In S81, low plant populations appear to have restricted the maximum GAI to about 0.8, from 850°Cd after sowing until GS31. Using Athene alone (the variety least affected by winter kill) the fit of the regression was improved when values after 850°Cd from sowing were excluded; this increased the percentage variance accounted for, from 67 per cent to 79 per cent to give the equation:

$$y = -\ 0.19\ (\pm\ 0.061) + 0.0009\ (\pm\ 0.00012)\ x,\ (r = 0.89,\ \text{d.f.} = 18)$$

3.3.2 Leaf longevity

When comparing different treatments and leaf positions on the mainstem, leaf longevity covered the range 18 to 100 days in calendar time and 80 to 660°Cd in thermal time. Before stem elongation there were normally only two live leaves unfolded at any one time, occasionally rising to three leaves when a new leaf unfolded (except in M. Otter),

or falling to one live leaf as the second youngest leaf died before the next unfolded (mainly M. Otter). After GS31 the number of live leaves rose to a maximum either when the flag leaf or its preceding leaf unfolded. The maximum ranged from four to six live leaves unfolded, dependant upon variety and sowing date (Athene had the most and M. Otter the least and S81 > S822 > S821). The number of live leaves began to fall, soon after the flag leaf unfolded, to zero before maturity.

The differences in leaf longevity between sowings and leaf position are illustrated in Figure 3.3.2. All S81 leaves unfolded before the equivalent leaf in S821 and all S821 before S822. All leaves, from leaf position 2 to 12 in S822, and 4 to 12 in S821, had a shorter duration than the equivalent leaf in S81 in terms of both calendar time and thermal time. For the initial leaves, the differences in thermal time were much smaller than in calendar time, as these covered the winter period. S822 leaves 9 to 12 lasted longer than equivalent S821 leaves. The severe winter of 1981-82 actually increased the longevity (^{o}Cd) of those leaves unfolded in the autumn but appeared to decrease the duration (^{o}Cd) of leaves which were extending during this period (leaves 4-6 in S821 and 2-4 in S822).

There was no consistent pattern to differences in individual leaf longevity between varieties, except for the often shorter duration of Maris Otter leaves. In S821 all Maris Otter leaves had a shorter duration than those on other varieties. After anthesis (leaves 8-12), Gerbel and Igri leaves lived longer than Athene in both S821 and S822, and Athene longer than Maris Otter in S822 and S81.

The shorter duration of Maris Otter leaves was in part a reflection of the disease and stress susceptibility of this cultivar. In S81 Maris Otter had the highest percentage of mildew (*Erysiphe graminis*) and rhynchosporium (*Rhynchosporium secalis*) on leaf 6 before spraying on 8 April. Again in S821 Maris Otter had the highest level of infection of mildew and rynchosporium before spraying on 20 April which would account for the short duration of leaves 5 and 6 in this treatment. In S822 Maris Otter again had a higher level of infection of rynchosporium and mildew than other

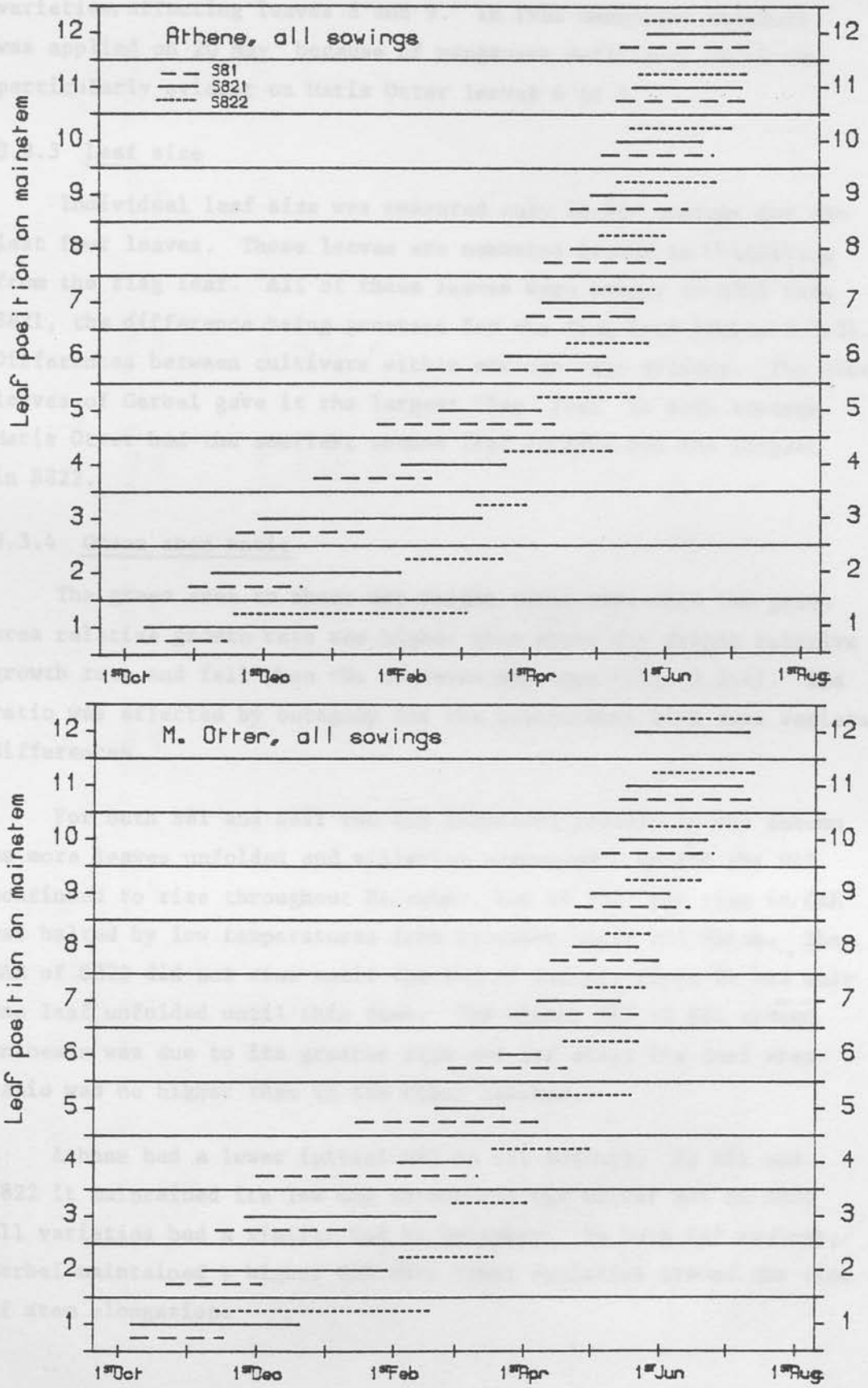

Fig. 3.3.2 Mainstem leaf longevity, from unfolding to death.

varieties, affecting leaves 8 and 9. In 1982 manganese sulphate was applied on 20 May because of manganese deficiency which was particularly evident on Maris Otter leaves 6 to 9.

3.3.3 Leaf size

Individual leaf size was measured only in S82 sowings for the last four leaves. These leaves are numbered from 1^{t} to 4^{t} starting from the flag leaf. All of these leaves were larger in S822 than S821, the difference being greatest for the flag leaf (Table 3.3.3). Differences between cultivars within sowings were evident. The wide leaves of Gerbel gave it the largest flag leaf in both sowings. Maris Otter had the smallest second leaf in S821 but the largest in S822.

3.3.4 Green area ratio

The green area to shoot dry weight ratio rose when the green area relative growth rate was higher than shoot dry weight relative growth rate and fell when the converse was true (Fig. 3.3.4). The ratio was affected by ontogeny and the environment with some varietal differences.

For both S81 and S821 the GAR increased rapidly in the autumn as more leaves unfolded and tillering commenced. In S81 the GAR continued to rise throughout December, but in S821 the rise in GAR was halted by low temperatures from December until mid-March. The GAR of S822 did not rise until the end of January since it had only one leaf unfolded until this time. The higher GAR of S81 around anthesis was due to its greater stem and ear area; its leaf area ratio was no higher than in the other sowings.

Athene had a lower initial GAR in all sowings. In S81 and S822 it maintained its low GAR throughout the winter but in S821 all varieties had a similar GAR by December. In both S82 sowings, Gerbel maintained a higher GAR than other varieties around the time of stem elongation.

TABLE 3.3.3: Leaf size

	Leaf 1^t (flag leaf)		Leaf 2^t		Leaf 3^t		Leaf 4^t	
	Length mm	Width mm	Length mm	Width mm	Length mm	Width mm	Length mm	Width mm
S821								
Gerbel	103	12.0	158	15.2	156	13.2	151	10.7
Athene	91	8.6	162	14.0	169	12.0	161	9.4
M. Otter	70	6.0	127	10.3	138	9.9	140	7.8
Igri	93	9.0	145	12.2	143	10.6	136	8.8
S822								
Gerbel	118	12.6	171	15.2	173	13.2	171	11.0
Athene	104	9.4	167	14.1	169	12.9	166	10.5
M. Otter	120	8.7	220	13.4	230	13.0	203	10.4
Igri	114	10.5	164	13.7	165	11.9	162	9.8
s.e. of mean (42 d.f.)	15.0	1.10	16.9	0.99	16.4	0.96	18.3	0.80
L.S.D. for treatment means (P = 0.05)	20.8	1.52	23.6	1.40	22.8	1.34	25.2	1.12

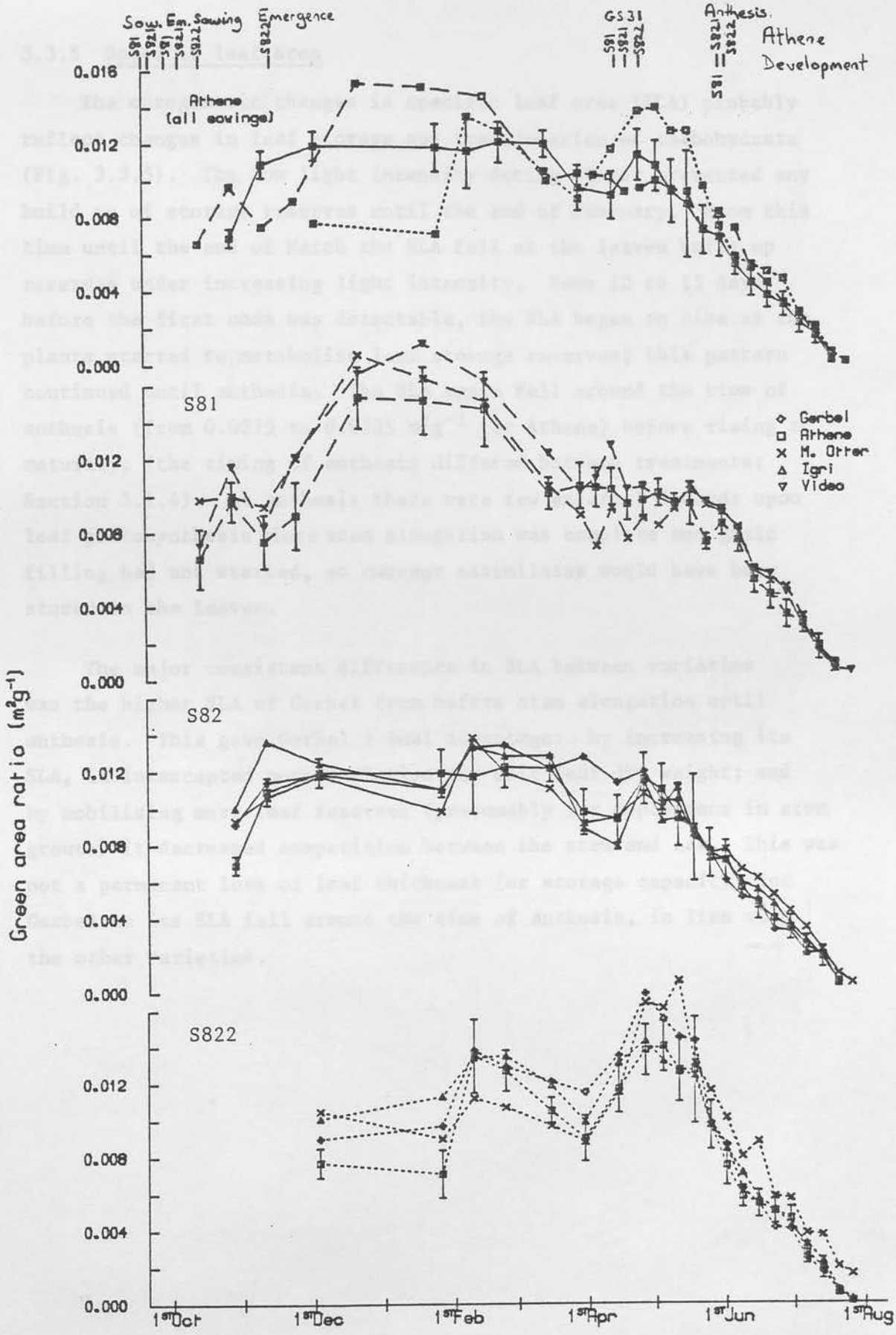

Fig. 3.3.4 Seasonal change in the green area ratio.
95% confidence limits for treatment mean shown on Athene.

3.3.5 Specific leaf area

The ontogenetic changes in specific leaf area (SLA) probably reflect changes in leaf storage and translocation of carbohydrate (Fig. 3.3.5). The low light intensity during winter prevented any build up of storage reserves until the end of February. From this time until the end of March the SLA fell as the leaves built up reserves under increasing light intensity. Some 10 to 15 days before the first node was detectable, the SLA began to rise as the plants started to metabolise leaf storage reserves; this pattern continued until anthesis. The SLA again fell around the time of anthesis (from 0.0275 to 0.0225 m^2g^{-1} for Athene) before rising to maturity, (the timing of anthesis differed between treatments; Section 3.1.4). At anthesis there were few external demands upon leaf photosynthesis since stem elongation was complete and grain filling had not started, so current assimilates would have been stored in the leaves.

The major consistent difference in SLA between varieties was the higher SLA of Gerbel from before stem elongation until anthesis. This gave Gerbel a dual advantage: by increasing its SLA, it intercepted more radiation per unit leaf dry weight; and by mobilising more leaf reserves (presumably for deployment in stem growth) it decreased competition between the stem and ear. This was not a permanent loss of leaf thickness (or storage capacity) for Gerbel as its SLA fell around the time of anthesis, in line with the other varieties.

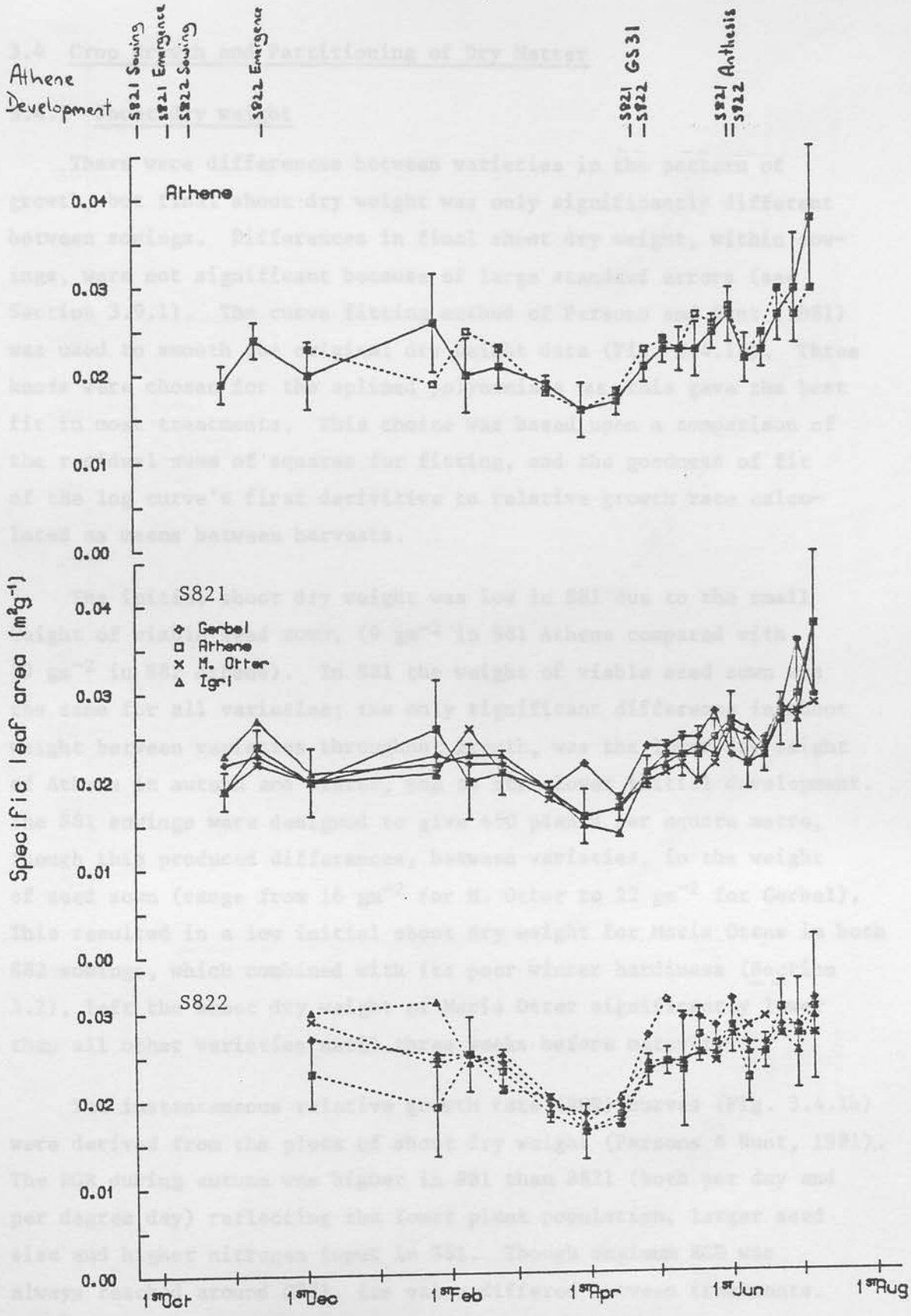

Fig. 3.3.5 Seasonal change in the specific leaf area.

3.4 Crop Growth and Partitioning of Dry Matter

3.4.1 Shoot dry weight

There were differences between varieties in the pattern of growth, but final shoot dry weight was only significantly different between sowings. Differences in final shoot dry weight, within sowings, were not significant because of large standard errors (see Section 3.9.1). The curve fitting method of Parsons and Hunt (1981) was used to smooth the original dry weight data (Fig. 3.4.1a). Three knots were chosen for the splined polynomials as this gave the best fit in most treatments. This choice was based upon a comparison of the residual sums of squares for fitting, and the goodness of fit of the log curve's first derivitive to relative growth rate calculated as means between harvests.

The initial shoot dry weight was low in S81 due to the small weight of viable seed sown, (9 gm^{-2} in S81 Athene compared with 19 gm^{-2} in S82 Athene). In S81 the weight of viable seed sown was the same for all varieties; the only significant difference in shoot weight between varieties throughout growth, was the lower dry weight of Athene in autumn and winter, due to its slower initial development. The S81 sowings were designed to give 450 plants per square metre, though this produced differences, between varieties, in the weight of seed sown (range from 16 gm^{-2} for M. Otter to 22 gm^{-2} for Gerbel). This resulted in a low initial shoot dry weight for Maris Otter in both S82 sowings, which combined with its poor winter hardiness (Section 3.2), left the shoot dry weight of Maris Otter significantly lower than all other varieties until three weeks before maturity.

The instantaneous relative growth rate (RGR) curves (Fig. 3.4.1b) were derived from the plots of shoot dry weight (Parsons & Hunt, 1981). The RGR during autumn was higher in S81 than S821 (both per day and per degree day) reflecting the lower plant population, larger seed size and higher nitrogen input in S81. Though maximum RGR was always reached around GS31, its value differed between treatments. The S822 maximum was significantly higher than either S81 or S821, though, in terms of relative growth rate per degree day the maximum value for S81 is raised closer to that of S822.

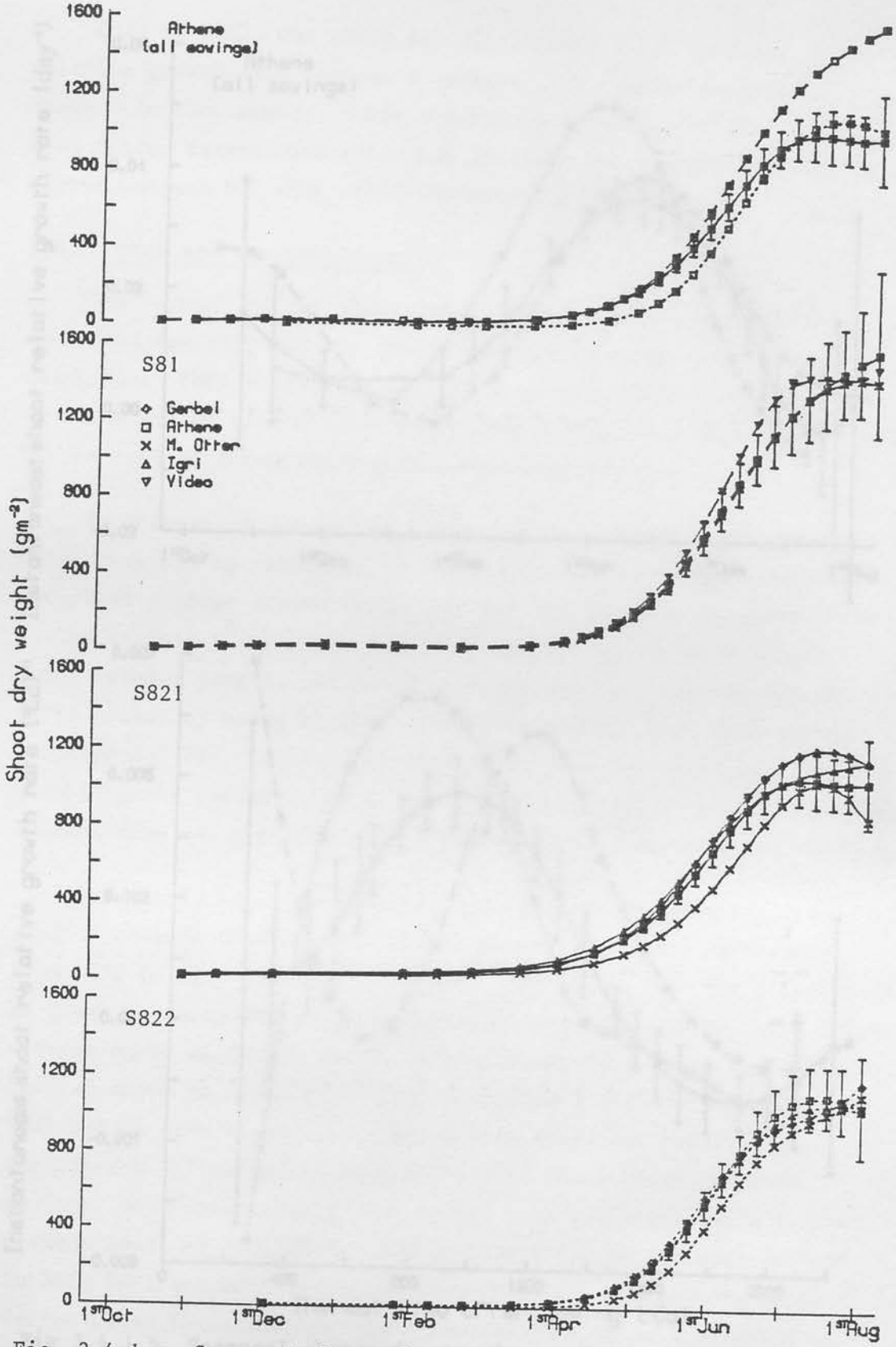

Fig. 3.4.1 a Seasonal change in the shoot dry weight. Fitted curves showing 95% confidence limits for Athene.

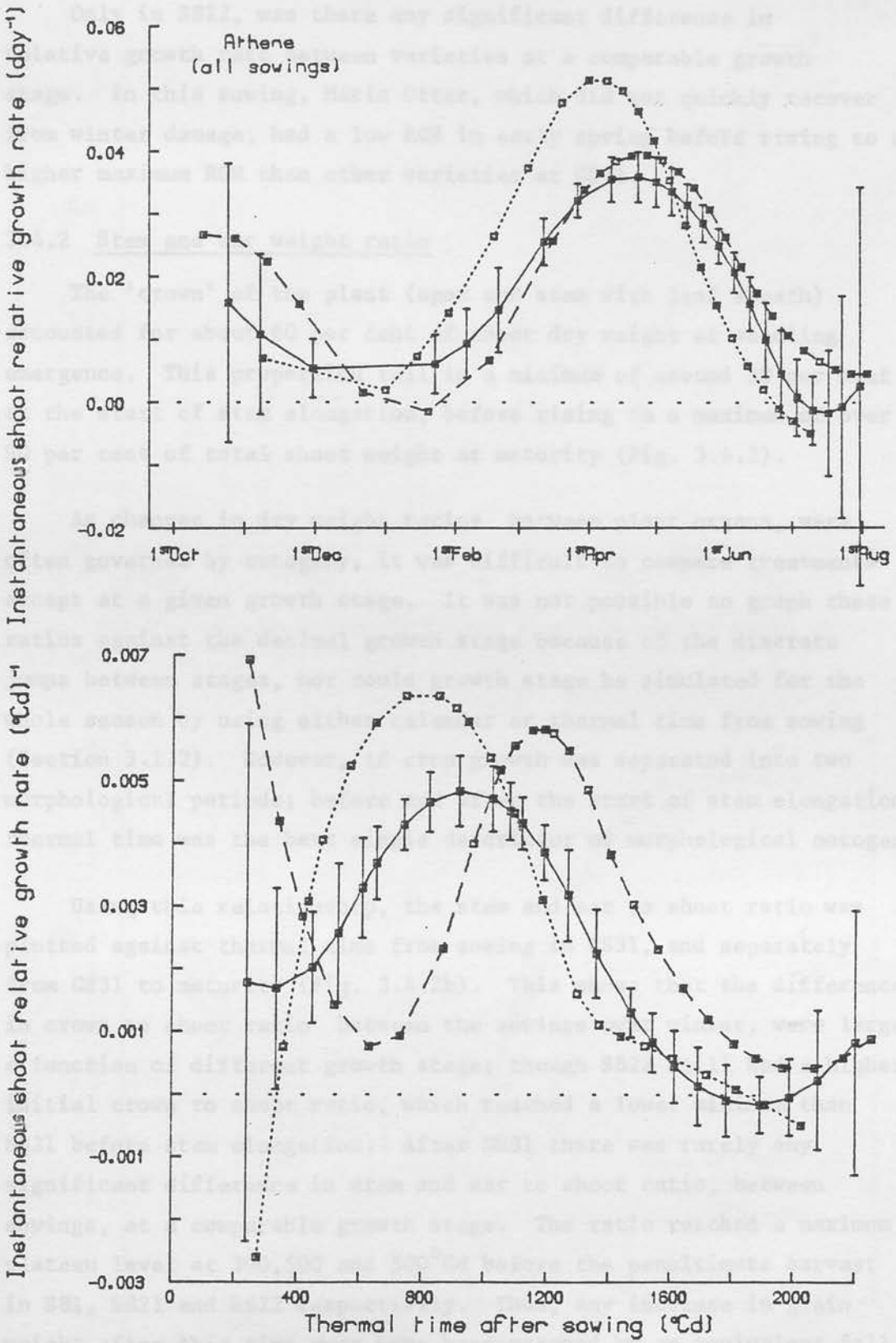

Fig 3.4.1 b Seasonal change in the shoot relative growth rate for Athene. Fitted curves showing the 95% confidence limits for S821.

Only in S822, was there any significant difference in relative growth rate between varieties at a comparable growth stage. In this sowing, Maris Otter, which did not quickly recover from winter damage, had a low RGR in early spring before rising to a higher maximum RGR than other varieties at GS31.

3.4.2 Stem and ear weight ratio

The 'crown' of the plant (apex and stem with leaf sheath) accounted for about 60 per cent of shoot dry weight at seedling emergence. This proportion fell to a minimum of around 30 per cent at the start of stem elongation, before rising to a maximum of over 90 per cent of total shoot weight at maturity (Fig. 3.4.2).

As changes in dry weight ratios between plant organs, were often governed by ontogeny, it was difficult to compare treatments except at a given growth stage. It was not possible to graph these ratios against the decimal growth stage because of the discrete jumps between stages, nor could growth stage be simulated for the whole season by using either calendar or thermal time from sowing (Section 3.1.2). However, if crop growth was separated into two morphological periods; before and after the start of stem elongation, thermal time was the best single descriptor of morphological ontogeny.

Using this relationship, the stem and ear to shoot ratio was plotted against thermal time from sowing to GS31, and separately from GS31 to maturity (Fig. 3.4.2b). This shows that the differences in crown to shoot ratio between the sowings over winter, were largely a function of different growth stage; though S822 still had a higher initial crown to shoot ratio, which reached a lower minimum than S821 before stem elongation. After GS31 there was rarely any significant difference in stem and ear to shoot ratio, between sowings, at a comparable growth stage. The ratio reached a maximum plateau level at 300,500 and 500^{o}Cd before the penultimate harvest in S81, S821 and S822 respectively. Thus, any increase in grain weight after this time must have been matched by an equivalent fall in stem weight, if it is assumed that there was no further increase in leaf weight.

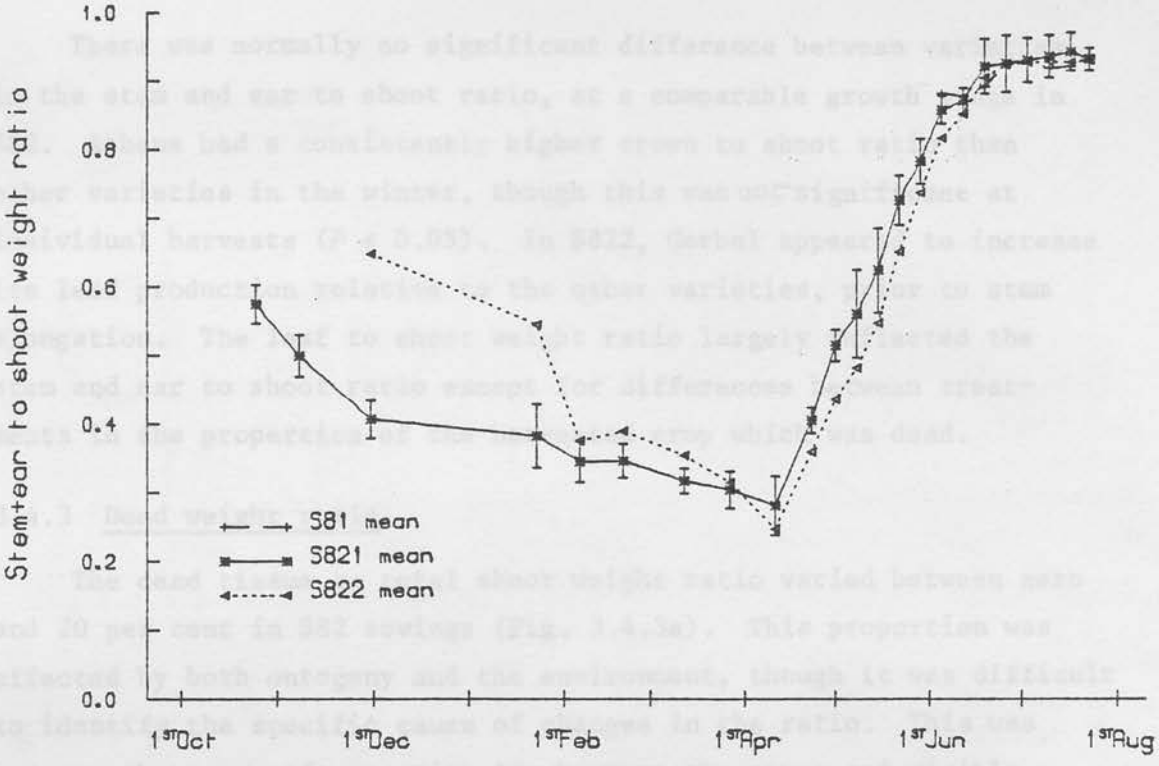

Fig. 3.4.2 a Seasonal change in the stem and ear to shoot weight ratio.

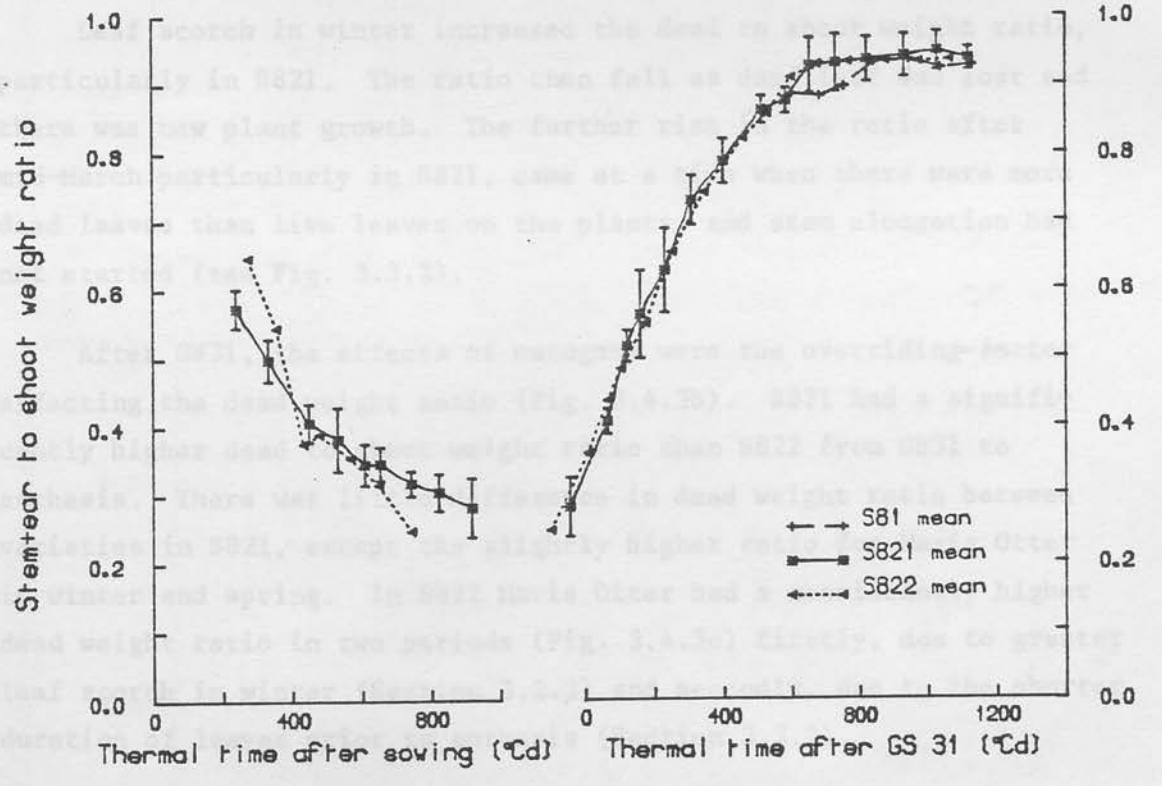

Fig. 3.4.2 b Change in the stem and ear to shoot weight ratio with thermal time after GS31.

There was normally no significant difference between varieties in the stem and ear to shoot ratio, at a comparable growth stage in S82. Athene had a consistently higher crown to shoot ratio than other varieties in the winter, though this was not significant at individual harvests ($P \leqslant 0.05$). In S822, Gerbel appeared to increase its leaf production relative to the other varieties, prior to stem elongation. The leaf to shoot weight ratio largely reflected the stem and ear to shoot ratio except for differences between treatments in the propertion of the harvested crop which was dead.

3.4.3 Dead weight ratio

The dead tissue to total shoot weight ratio varied between zero and 20 per cent in S82 sowings (Fig. 3.4.3a). This proportion was affected by both ontogeny and the environment, though it was difficult to identify the specific cause of changes in the ratio. This was because there was often a time lag between the cause and visible effect of senescence, and because dead material could still be attached to the plant many weeks after senescence.

Leaf scorch in winter increased the dead to shoot weight ratio, particularly in S821. The ratio then fell as dead leaf was lost and there was new plant growth. The further rise in the ratio after mid-March particularly in S821, came at a time when there were more dead leaves than live leaves on the plants, and stem elongation had not started (see Fig. 3.3.2).

After GS31, the effects of ontogeny were the overriding factor affecting the dead weight ratio (Fig. 3.4.3b). S821 had a significantly higher dead to shoot weight ratio than S822 from GS31 to anthesis. There was little difference in dead weight ratio between varieties in S821, except the slightly higher ratio for Maris Otter in winter and spring. In S822 Maris Otter had a consistently higher dead weight ratio in two periods (Fig. 3.4.3c) firstly, due to greater leaf scorch in winter (Section 3.2.2) and secondly, due to the shorter duration of leaves prior to anthesis (Section 3.3.2).

3.4.4 Grain weight ratio

The grain to shoot dry weight ratio is shown in Figure 3.4.4a against thermal time after anthesis, rather than calendar time, to

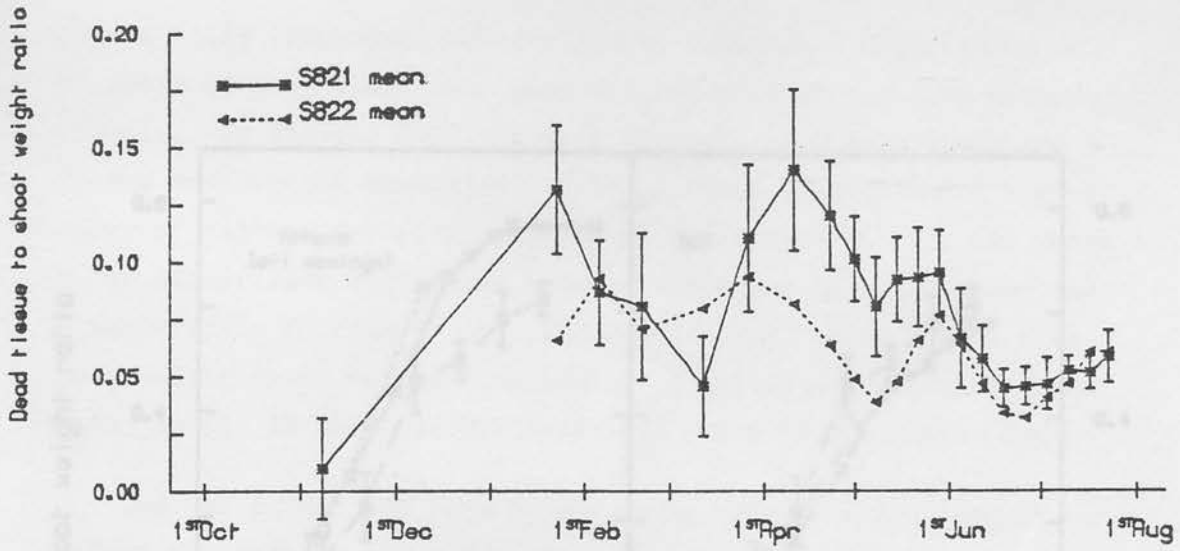

Fig 3.4.3 a Seasonal change in the dead tissue to shoot weight ratio.

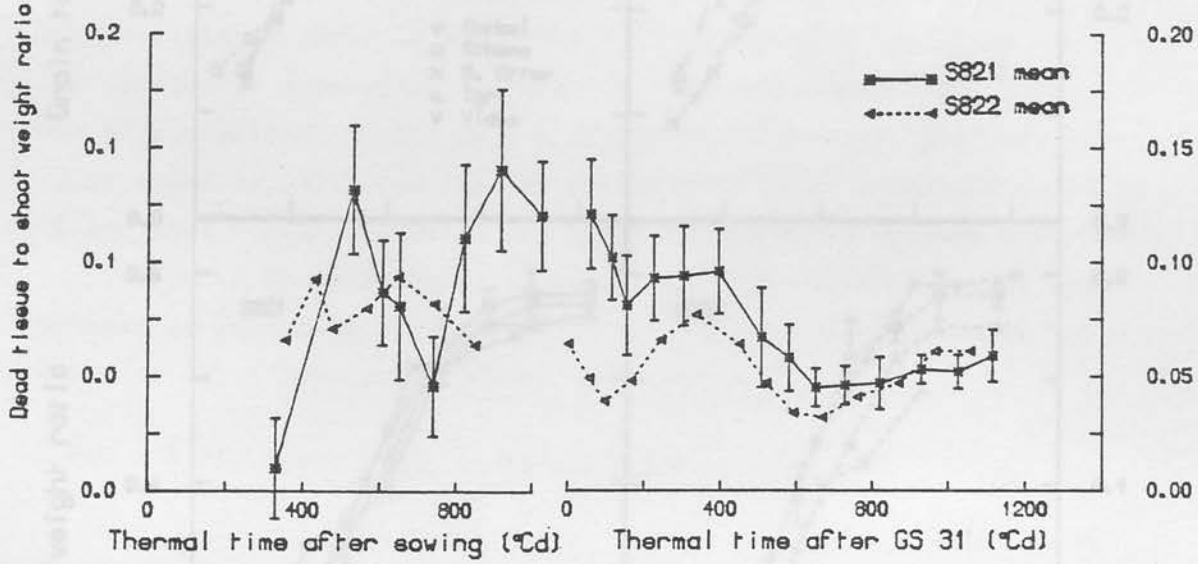

Fig 3.4.3 b Change in the dead tissue to shoot weight ratio with thermal time.

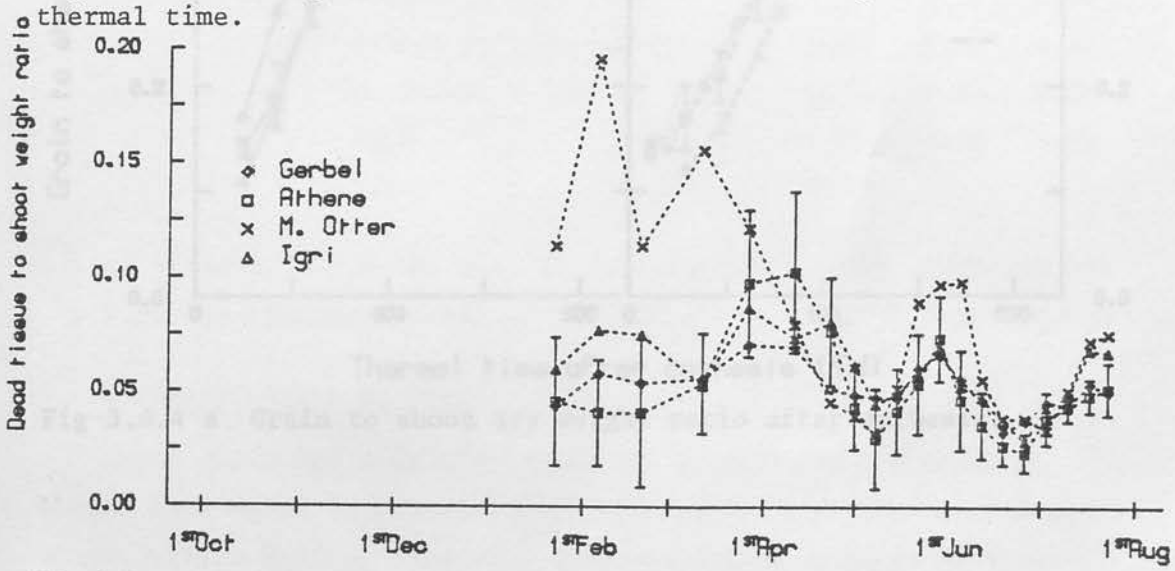

Fig 3.4.3 c Seasonal change in the dead tissue to shoot weight ratio in S822.

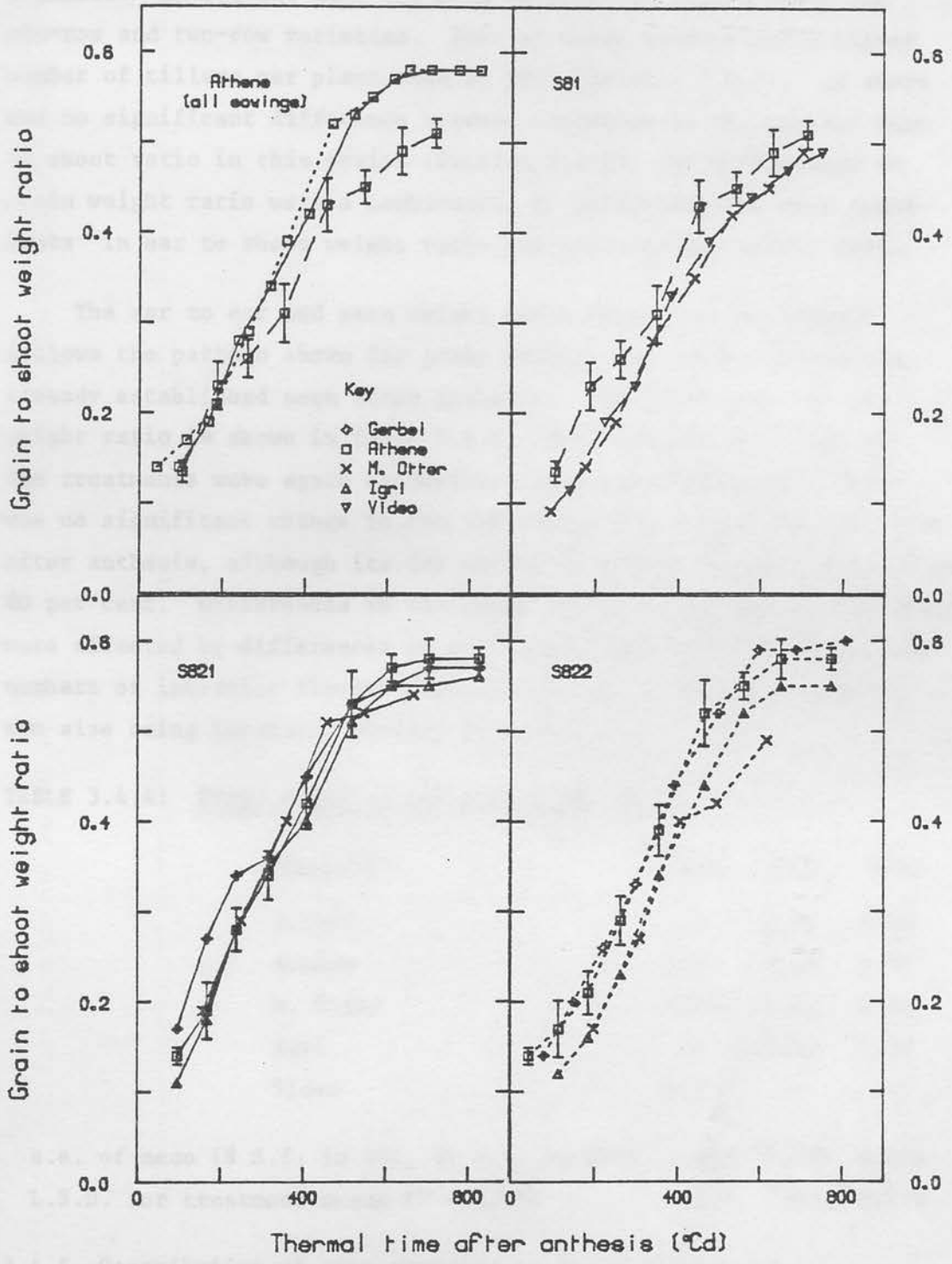

Fig 3.4.4 a Grain to shoot dry weight ratio after anthesis.

allow a valid comparison of treatments. The major differences in the ratio between varieties, were already established soon after anthesis. In S81 and S822 the main differences were between the six-row and two-row varieties. Both of these sowings had a higher number of tillers per plant than in S821 (Section 3.6.3). As there was no significant difference between varieties in the ear and stem to shoot ratio in this period (Section 3.4.2), the differences in grain weight ratio were a combination of differences between treatments in ear to shoot weight ratio and grain to ear weight ratio.

The ear to ear and stem weight ratio (Fig. 3.4.4b) largely follows the pattern shown for grain weight ratio with differences already established soon after anthesis. The final grain to ear weight ratio is shown in Table 3.4.4. The relative positions of the treatments were again established soon after anthesis. There was no significant change in awn and rachis dry weight per unit area after anthesis, although its dry matter percentage doubled from 40 to 80 per cent. Differences in the grain to ear ratio between treatments, were affected by differences in crop structure (Section 3.6.3), and numbers of infertile florets (Section 3.7.2), with differences in awn size being important between varieties.

TABLE 3.4.4: Final grain to ear dry weight ratio

Variety	S81	S821	S822
Gerbel	-	0.91	0.90
Athene	0.87	0.88	0.87
M. Otter	0.88	0.89	0.86
Igri	-	0.90	0.87
Video	0.87	-	-
s.e. of mean (9 d.f. in S81, 21 d.f. in S82)	0.015	0.004	0.004
L.S.D. for treatment means (P = 0.05)	0.023	0.006	0.006

3.4.5 Contribution of stem reserves to grain filling

Both grain and stem dry weight after anthesis are shown as sowing date means in Figure 3.4.5. The variations in stem and grain weight within sowings were much less than those between sowings.

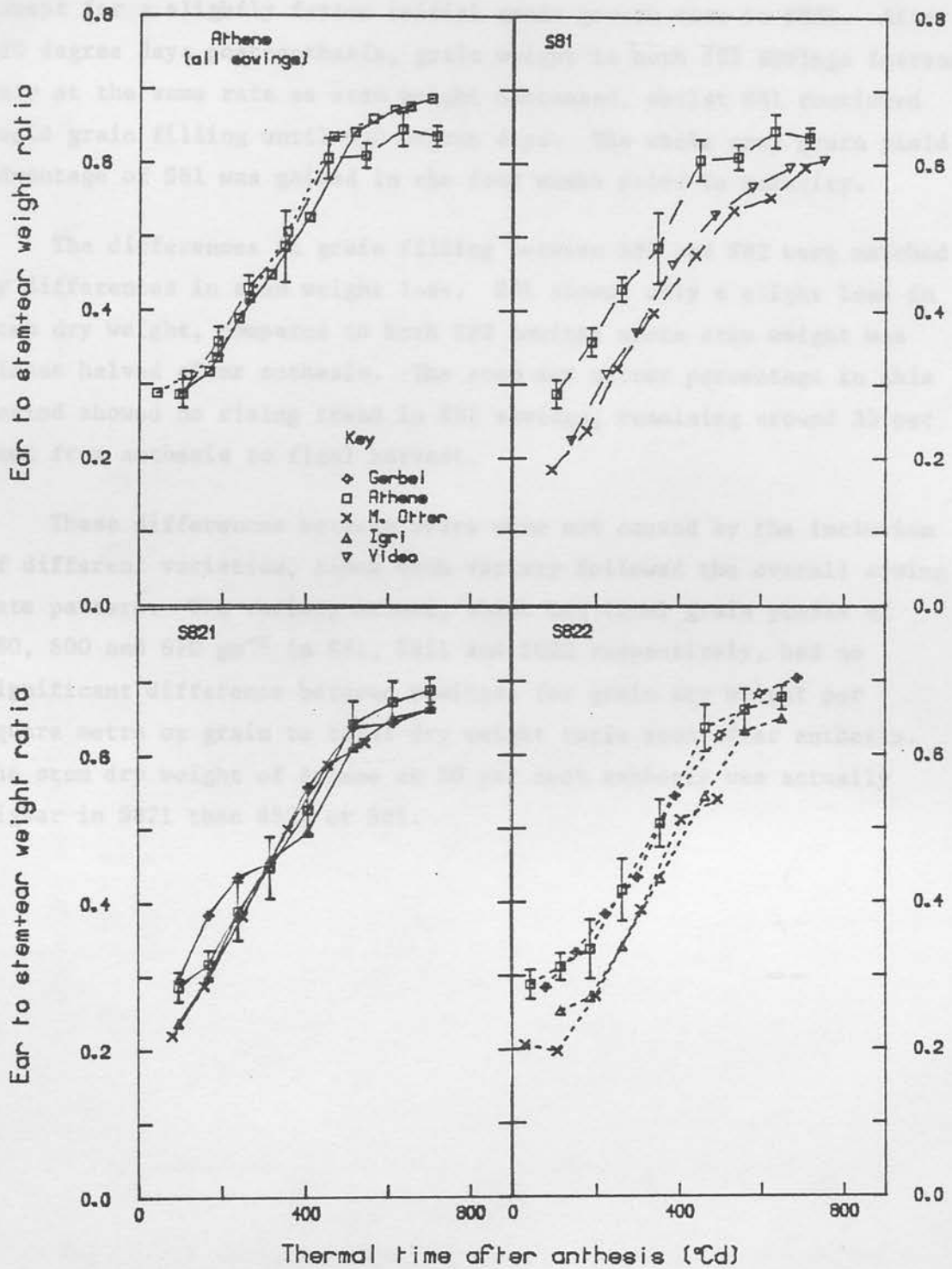

Fig 3.4.4 b Ear to stem plus ear dry weight ratio after anthesis.

Initial grain dry weight was similar for all sowings, as was the rate of grain growth up to 450 degree days after anthesis ($\simeq$ 5 weeks), except for a slightly faster initial grain growth rate in S821. After 450 degree days post-anthesis, grain weight in both S82 sowings increased only at the same rate as stem weight decreased, whilst S81 continued rapid grain filling until 650 degree days. The whole crop grain yield advantage of S81 was gained in the four weeks prior to maturity.

The differences in grain filling between S81 and S82 were matched by differences in stem weight loss. S81 showed only a slight loss in stem dry weight, compared to both S82 sowings where stem weight was almost halved after anthesis. The stem dry matter percentage in this period showed no rising trend in S82 sowings, remaining around 33 per cent from anthesis to final harvest.

These differences between years were not caused by the inclusion of different varieties, since each variety followed the overall sowing date pattern. The variety Athene, which had final grain yields of 880, 600 and 670 gm^{-2} in S81, S821 and S822 respectively, had no significant difference between sowings, for grain dry weight per square metre or grain to total dry weight ratio soon after anthesis. The stem dry weight of Athene at 50 per cent anthesis was actually higher in S821 than S822 or S81.

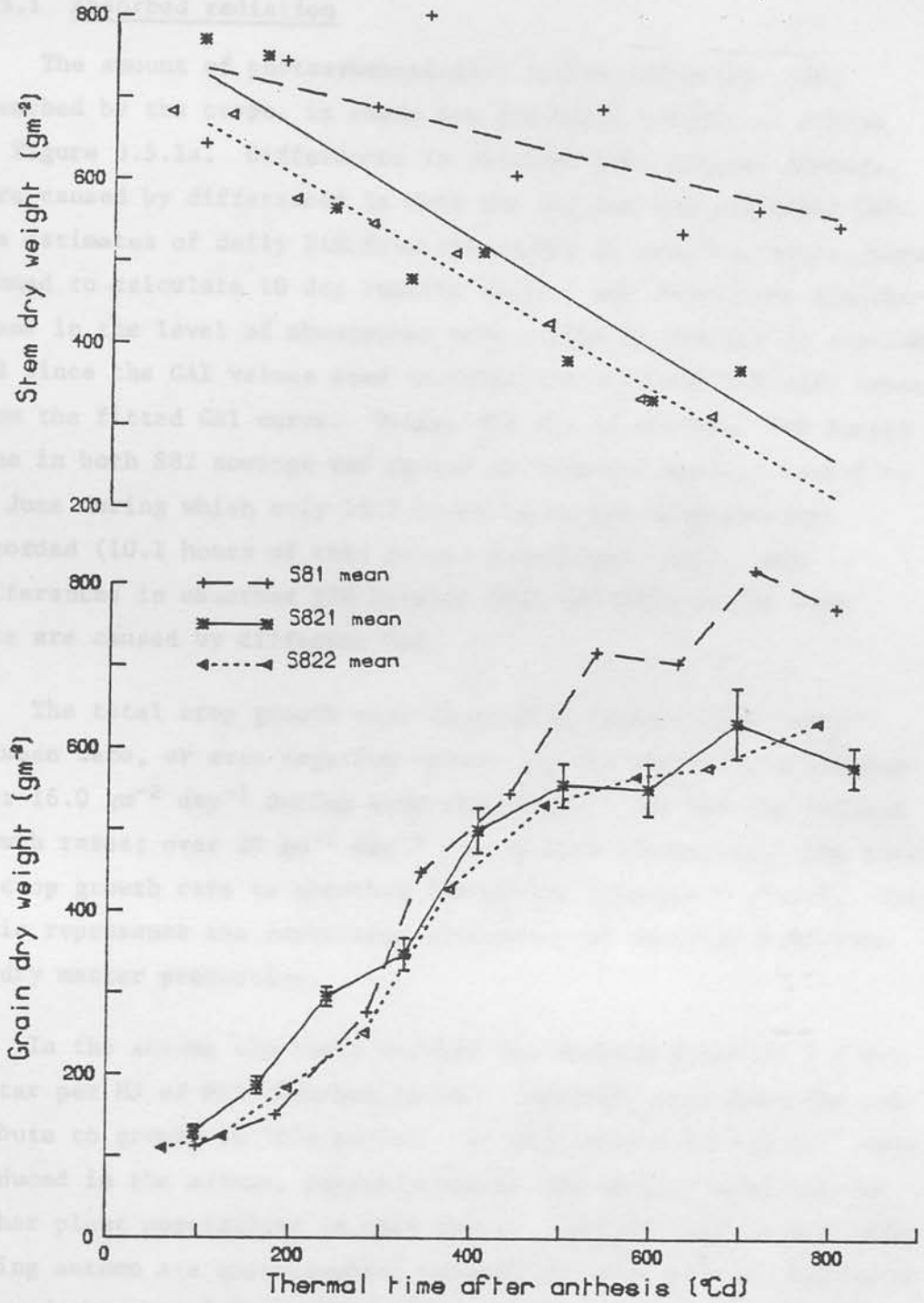

Fig. 3.4.5 Change in the stem and grain weight after anthesis.
Fitted lines for stem dry weight:
S81, $y = 760(\pm 56) - 0.25(\pm 0.11)x$;
S821, $y = 800(\pm 54) - 0.74(\pm 0.13)x$;
S822, $y = 730(\pm 16) - 0.64(\pm 0.039)x$.

3.5 Absorbed Radiation and Crop Growth

3.5.1 Absorbed radiation

The amount of photosynthetically active radiation (PAR) absorbed by the crops, is shown for the three sowings of Athene in Figure 3.5.1a. Differences in absorbed PAR between sowings, were caused by differences in both the GAI and the available PAR. The estimates of daily PAR from the number of sunshine hours, were summed to calculate 10 day running means. Any short-term fluctuations in the level of absorption were caused by changes in available PAR since the GAI values used to calculate absorbed PAR were taken from the fitted GAI curve. Hence, the dip in absorbed PAR during June in both S82 sowings was caused by overcast weather from 9 to 26 June during which only 15.7 hours of bright sunshine were recorded (10.1 hours of this on one exceptional day). Any differences in absorbed PAR between S821 and S822 on the same date are caused by different GAI.

The total crop growth rate (including roots) (CGR) varied between zero, or even negative values in the winter to a maximum over 16.0 gm^{-2} day^{-1} during stem elongation. S81 had the highest growth rates; over 20 gm^{-2} day^{-1} during stem elongation. The ratio of crop growth rate to absorbed PAR varied throughout growth. This ratio represents the conversion efficiency of absorbed radiation to dry matter production.

In the autumn the ratio reached its maximum value of 7 g dry matter per MJ of PAR absorbed in S81. However, seed reserves contribute to growth in this period. In S821 only 4 to 6 g MJ^{-1} were produced in the autumn, possibly due to the smaller seed size or higher plant populations in this sowing. Differences in the ratio during autumn are questionable, because the low absolute values of CGR and absorbed PAR at this time, mean that any error made in estimating either was multiplied in calculating the ratio. The ratio fell rapidly after the third leaf unfolded, around the start of December, to zero by the beginning of January. No data were available for S822 in the autumn and winter because only one harvest was taken before the end of January in this sowing. The ratio of CGR

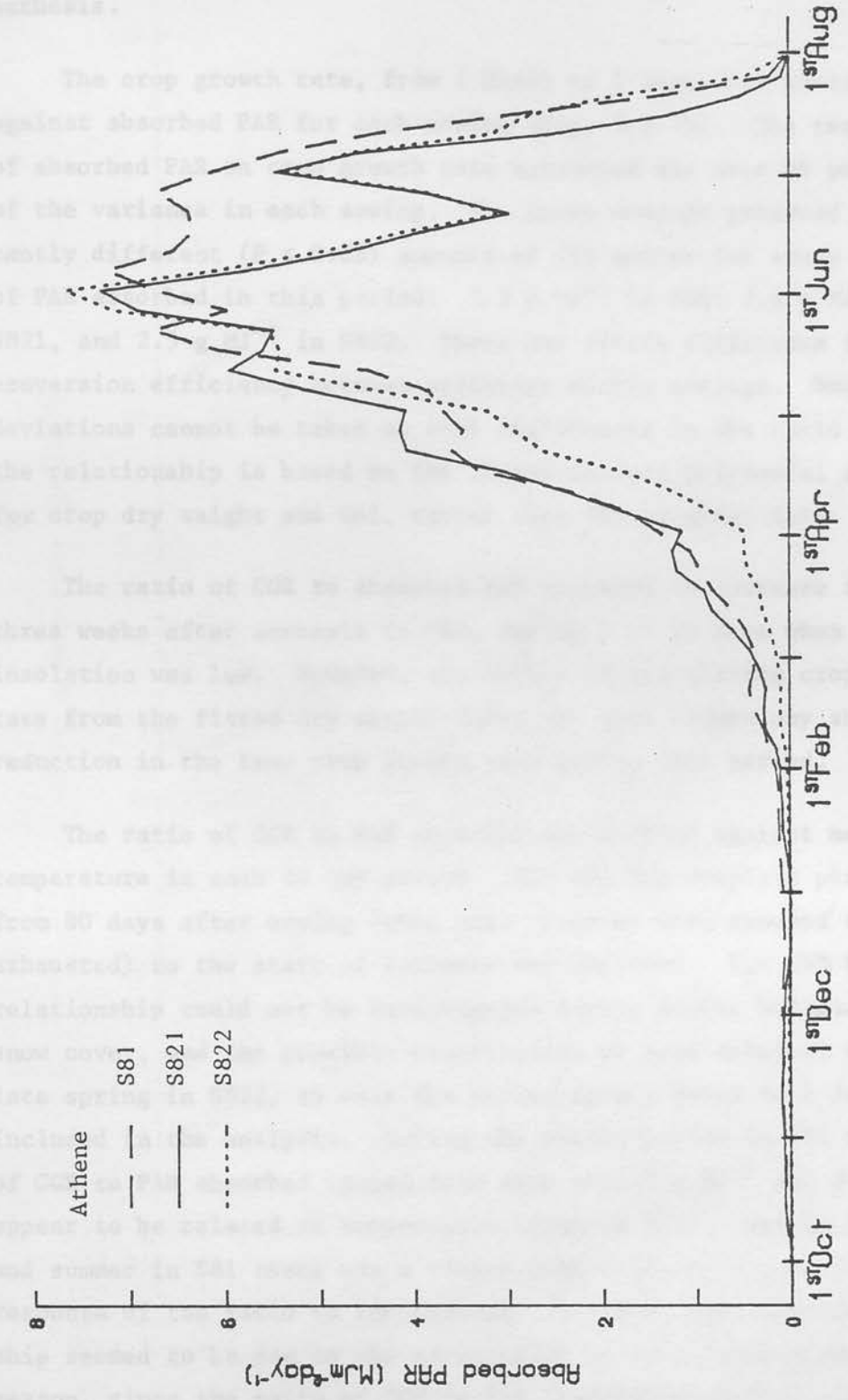

Fig. 3.5.1 a Seasonal change in absorbed PAR.

to PAR absorbed rose throughout February to reach 2 to 3 g MJ^{-1} at the beginning of March, and remained around this level until anthesis.

The crop growth rate, from 1 March to 1 June, was plotted against absorbed PAR for each sowing (Fig. 3.5.1b). The regression of absorbed PAR on crop growth rate accounted for over 95 per cent of the variance in each sowing. The three sowings produced significantly different ($P \leq 0.05$) amounts of dry matter for every 1.0 MJ of PAR absorbed in this period: 3.2 g MJ^{-1} in S81; 2.4 g MJ^{-1} in S821, and 2.5 g MJ^{-1} in S822. There was little difference in the conversion efficiency between varieties within sowings. Small deviations cannot be taken as real differences in the ratio since the relationship is based on the fitted splined polynomial curves for crop dry weight and GAI, rather than the original data.

The ratio of CGR to absorbed PAR appeared to increase for three weeks after anthesis in S82, during 9 to 26 June when insolation was low. However, the method of calculating crop growth rate from the fitted dry weight curve may have hidden any short-term reduction in the true crop growth rate during this period.

The ratio of CGR to PAR absorbed was plotted against mean temperature in each 10 day period. For S81 the complete period from 80 days after sowing (when seed reserves were assumed to be exhausted) to the start of anthesis was included. For S82 the relationship could not be investigated during winter because of snow cover, and the possible contribution of seed reserves until late spring in S822, so only the period from 1 March to 1 June was included in the analysis. During the winter period in S81 the ratio of CGR to PAR absorbed ranged from zero to 2.0 g MJ^{-1} and did not appear to be related to temperature (range 0-6^{o}C). During spring and summer in S81 there was a slight suggestion of a positive response of the ratio to temperature. However, this apparent relationship seemed to be due to the correlation between temperature and season, since the ratio of CGR to PAR absorbed increased slightly between 1 March and 1 June, in this sowing. Between 1 March and 1 June in S82 the ratio ranged from 1.8 to 4.0 g MJ^{-1} and covered a 10 day mean temperature range of 3 to 16^{o}C. There was no apparent

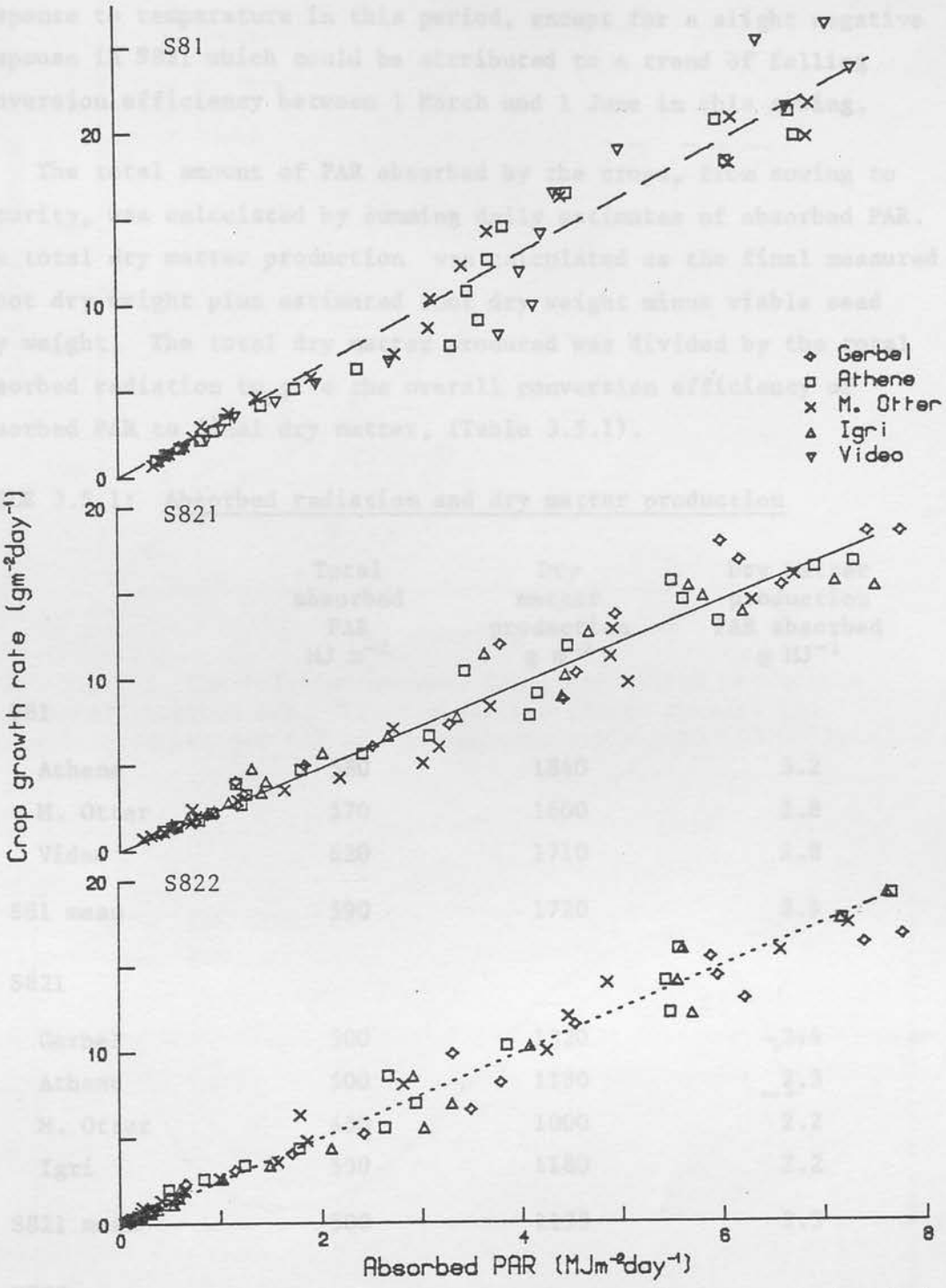

Fig. 3.5.1 b The relation between crop growth rate and absorbed PAR between 1 March and 1 June. The fitted lines were forced through the origin and accounted for 96, 95 and 98% of the variance respectively. S81 : $y = 3.20(\pm 0.050)x$. S821 : $y = 2.40(\pm 0.031)x$. S821 : $y = 2.45(\pm 0.027)x$.

response to temperature in this period, except for a slight negative response in S821 which could be attributed to a trend of falling conversion efficiency between 1 March and 1 June in this sowing.

The total amount of PAR absorbed by the crops, from sowing to maturity, was calculated by summing daily estimates of absorbed PAR. The total dry matter production was calculated as the final measured shoot dry weight plus estimated root dry weight minus viable seed dry weight. The total dry matter produced was divided by the total absorbed radiation to give the overall conversion efficiency of absorbed PAR to final dry matter, (Table 3.5.1).

TABLE 3.5.1: Absorbed radiation and dry matter production

	Total absorbed PAR MJ m^{-2}	Dry matter production g m^{-2}	Dry matter production PAR absorbed g MJ^{-1}
S81			
Athene	580	1840	3.2
M. Otter	570	1600	2.8
Video	620	1710	2.8
S81 mean	590	1720	2.9
S821			
Gerbel	500	1220	2.4
Athene	500	1130	2.3
M. Otter	450	1000	2.2
Igri	530	1180	2.2
S821 mean	500	1133	2.3
S822			
Gerbel	480	1300	2.7
Athene	450	1270	2.8
M. Otter	460	1210	2.6
Igri	480	1210	2.5
S822 mean	470	1250	2.7

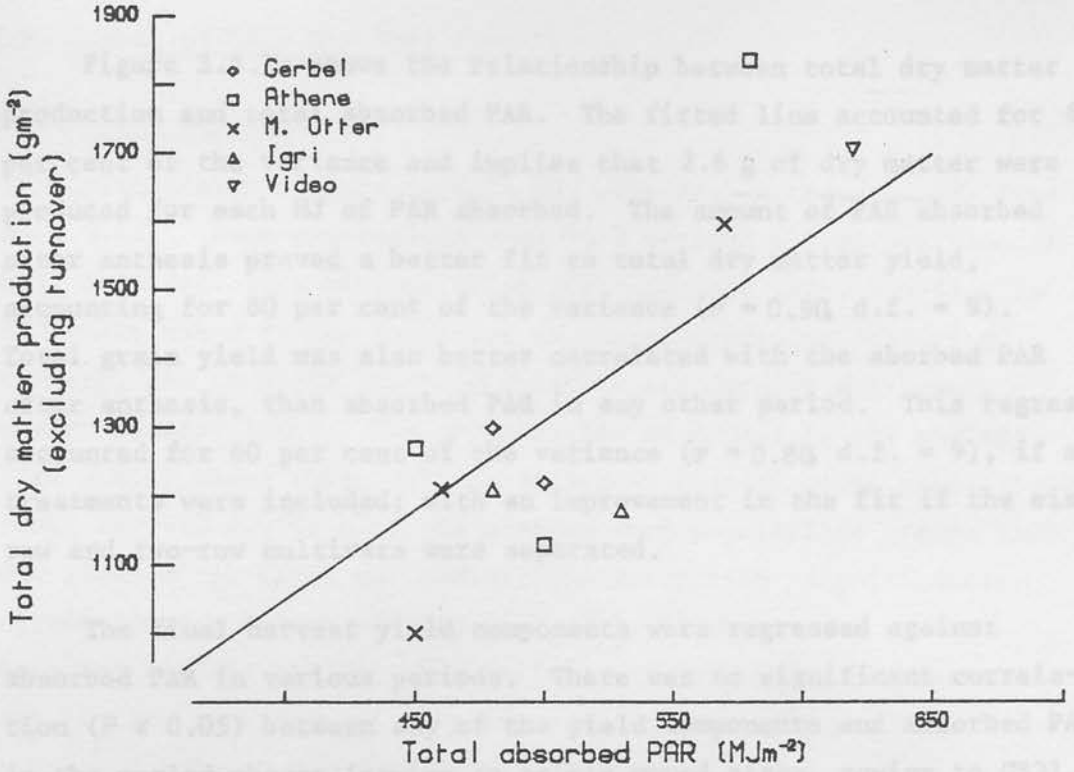

Fig. 3.5.1 c The relation between total dry matter production and total absorbed PAR. The fitted line forced through the origin accounted for 64% of the variance : y = 2.63 (±0.093)x.

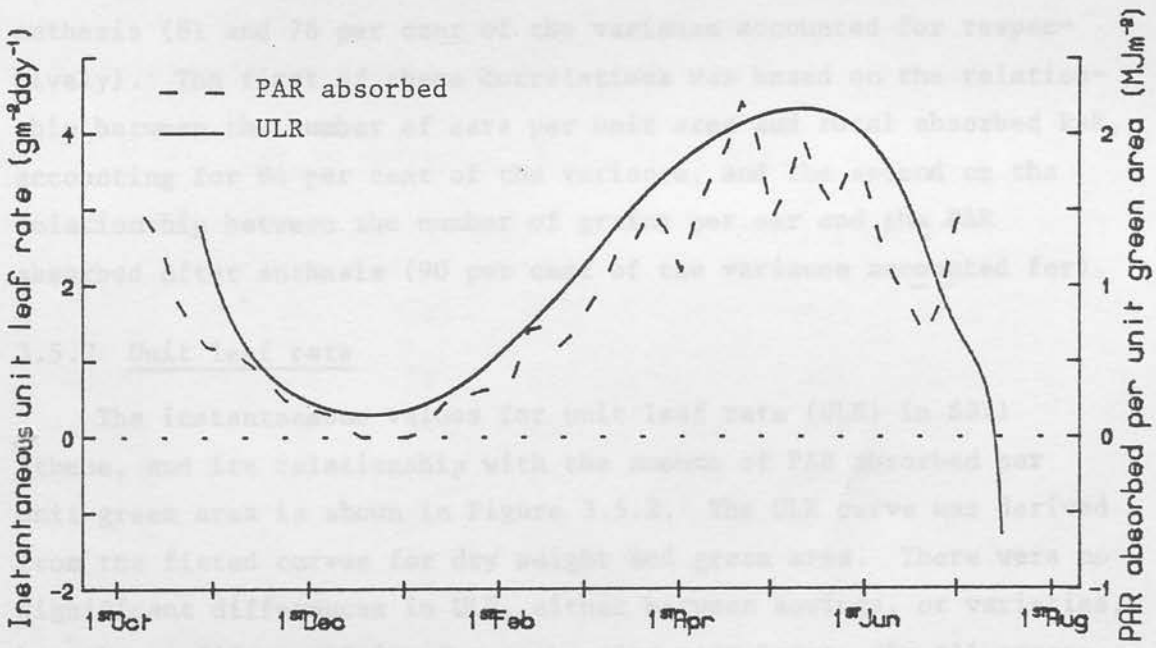

Fig. 3.5.2 Seasonal change in the unit leaf rate and absorbed PAR per unit green area.

Figure 3.5.1c shows the relationship between total dry matter production and total absorbed PAR. The fitted line accounted for 64 per cent of the variance and implies that 2.6 g of dry matter were produced for each MJ of PAR absorbed. The amount of PAR absorbed after anthesis proved a better fit to total dry matter yield, accounting for 80 per cent of the variance ($r = 0.90$, d.f. = 9). Total grain yield was also better correlated with the aborbed PAR after anthesis, than absorbed PAR in any other period. This regression accounted for 60 per cent of the variance ($r = 0.80$, d.f. = 9), if all treatments were included; with an improvement in the fit if the six-row and two-row cultivars were separated.

The final harvest yield components were regressed against absorbed PAR in various periods. There was no significant correlation ($P \leq 0.05$) between any of the yield components and absorbed PAR in the periods chosen (sowing to triple mound stage, sowing to GS31, sowing to anthesis, sowing to maturity, GS31 to anthesis, and anthesis to maturity) when all treatments were analysed together. However, for the six-row cultivars, the number of grains per unit ground area was correlated with both total absorbed PAR and PAR absorbed after anthesis (81 and 76 per cent of the variance accounted for respectively). The first of these correlations was based on the relationship between the number of ears per unit area and total absorbed PAR, accounting for 84 per cent of the variance, and the second on the relationship between the number of grains per ear and the PAR absorbed after anthesis (90 per cent of the variance accounted for).

3.5.2 Unit leaf rate

The instantaneous values for unit leaf rate (ULR) in S821 Athene, and its relationship with the amount of PAR absorbed per unit green area is shown in Figure 3.5.2. The ULR curve was derived from the fitted curves for dry weight and green area. There were no significant differences in ULR, either between sowings, or varieties, but the confidence limits for each point were large. In all treatments, ULR was initially high, fell to near zero in mid-winter and rose to a maximum at the time of maximum crop growth rate during stem elongation, before falling at the end of the season. Most of the variation in ULR appears to have been the result of seasonal variation in the amount of PAR absorbed per unit green area.

3.6 Number of Ears per Unit Area

3.6.1 Stem population

Initial plant populations in S82 were double those of S81 (see Table 2.1a). Stem populations rose to a maximum around the time of GS31, then fell to a minimum value near anthesis (Fig. 3.6.1). In S822 there was a marked reduction in the stem population during February, due to plant death in December and January which only became apparent later. The presentation of Athene in all sowings (Fig. 3.6.1) shows that, despite different initial plant populations (range 160-410 plants m^{-2}) and maximum stem populations (range 1100-2200 stems m^{-2}), final ear numbers did not differ significantly between sowings (range 400-460 ears m^{-2}). Although the two-row varieties did not exhibit this uniform ear population between sowings, tiller survival was more important than tiller production in deciding final ear numbers, in all treatments.

3.6.2 Tiller production

In S81 and S821 the first tiller emerged in the autumn, but in S822 no tillers emerged until the spring. The differences between sowings and varieties in the time to tiller emergence (GS21) could not be completely removed by using thermal time (Table 3.6.2a).

TABLE 3.6.2a: Time to emergence of the first tiller (GS21)

Variety	Calendar time (days after sowing)			Thermal time (^{o}Cd after sowing)		
	S81	S821	S822	S81	S821	S822
Gerbel	-	68	152	-	435	566
Athene	54	64	156	422	415	581
M. Otter	47	72	165	389	448	637
Igri	-	64	151	-	415	567
Video	47	-	-	389	-	-

From GS21 to the time of maximum stem population, the rates of tiller emergence per plant were approximately linear in thermal time (Table 3.6.2b). The difference between varieties and sowing dates in the rate of tiller emergence were similar to those for mainstem leaf emergence, with later sowings tillering at faster rates. On

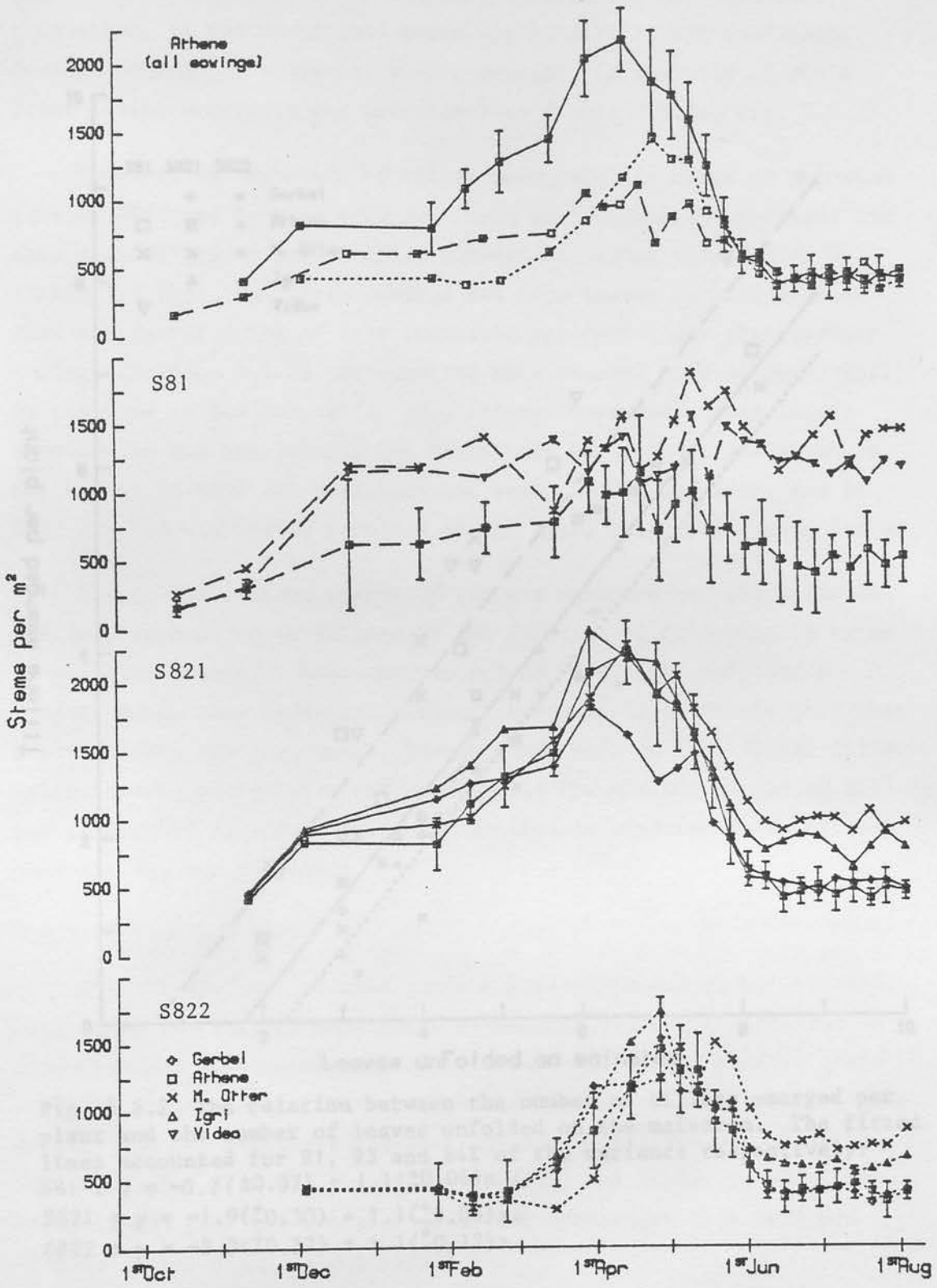

Fig. 3.6.1 Seasonal change in the stem population.

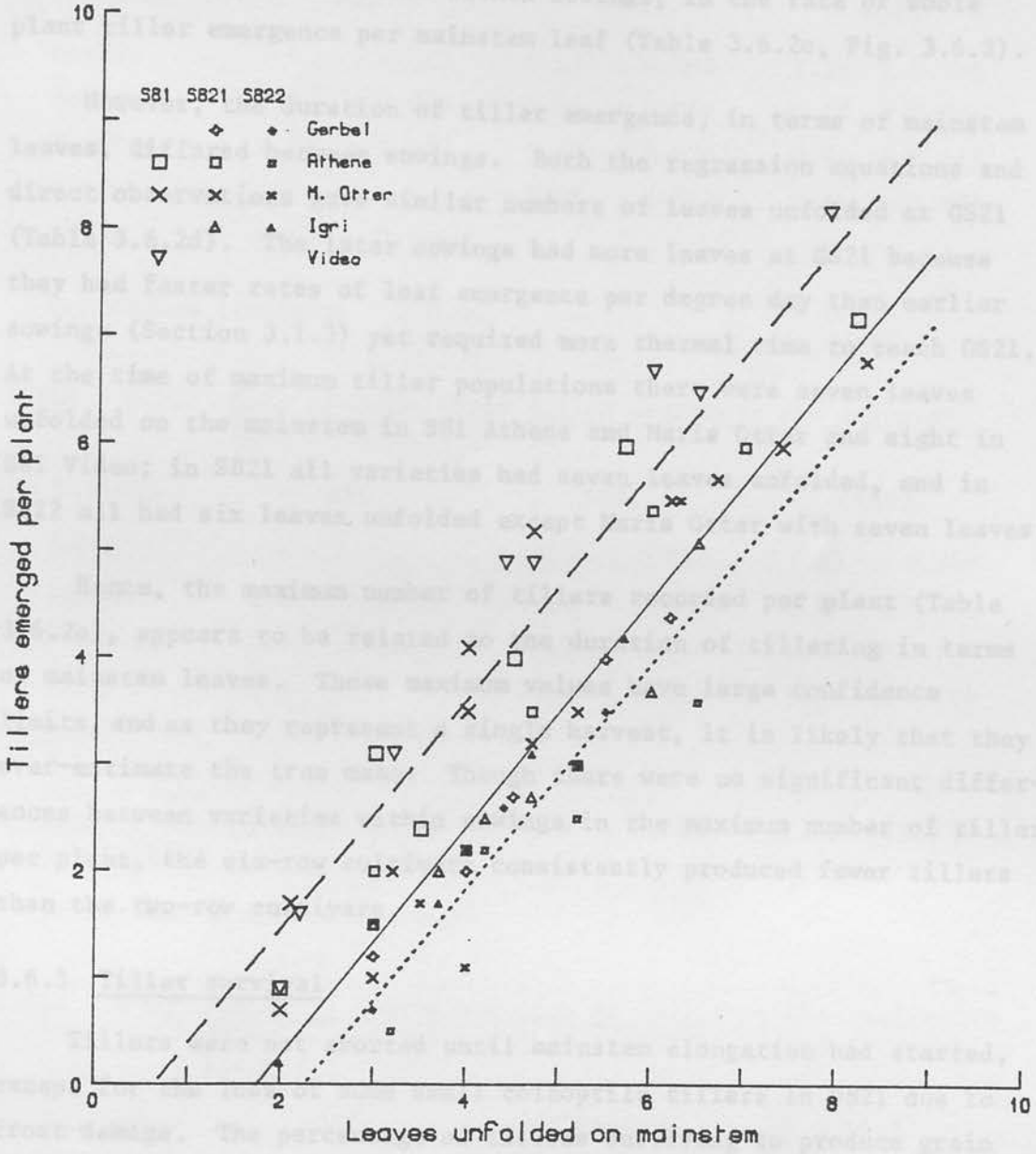

Fig. 3.6.2 The relation between the number of tillers emerged per plant and the number of leaves unfolded on the mainstem. The fitted lines accounted for 91, 93 and 84% of the variance respectively:
S81 : $y = -0.7(\pm 0.37) + 1.1(\pm 0.06)x$.
S821 : $y = -1.9(\pm 0.30) + 1.1(\pm 0.06)x$.
S822 : $y = -2.3(\pm 0.57) + 1.1(\pm 0.12)x$.

examining this relationship between tillering and mainstem leaf production, it was found that there was no significant difference between sowings, or varieties within sowings, in the rate of whole plant tiller emergence per mainstem leaf (Table 3.6.2c, Fig. 3.6.2).

However, the duration of tiller emergence, in terms of mainstem leaves, differed between sowings. Both the regression equations and direct observations gave similar numbers of leaves unfolded at GS21 (Table 3.6.2d). The later sowings had more leaves at GS21 because they had faster rates of leaf emergence per degree day than earlier sowings (Section 3.1.3) yet required more thermal time to reach GS21. At the time of maximum tiller populations there were seven leaves unfolded on the mainstem in S81 Athene and Maris Otter and eight in S81 Video; in S821 all varieties had seven leaves unfolded, and in S822 all had six leaves unfolded except Maris Otter with seven leaves.

Hence, the maximum number of tillers recorded per plant (Table 3.6.2e), appears to be related to the duration of tillering in terms of mainstem leaves. These maximum values have large confidence limits, and as they represent a single harvest, it is likely that they over-estimate the true mean. Though there were no significant differences between varieties within sowings in the maximum number of tillers per plant, the six-row cultivars consistently produced fewer tillers than the two-row cultivars.

3.6.3 Tiller survival

Tillers were not aborted until mainstem elongation had started, except for the loss of some small coleoptile tillers in S821 due to frost damage. The percentage of tillers surviving to produce grain was much higher in the two-row than the six-row cultivars, and higher in S81 than S82 despite the greater number of tillers per plant in S81 (Table 3.6.3). The percentage survival was higher in S822 than S821, though S821 had a higher final ear population than S822 due largely to its higher plant population.

All tillers which survived to ear emergence bore grain, though for the six-row cultivars even tillers which were 'in boot' (GS45), died if they had not emerged when anthesis was complete in the mainstem.

TABLE 3.6.2b: Rate of tiller emergence (tillers per plant per 100 degree days) (from GS21 to maximum tiller number)

Variety	S81	S821	S822
Gerbel	-	0.62 ± 0.048	1.23 ± 0.250
Athene	0.63 ± 0.063	0.66 ± 0.066	0.77 ± 0.201
M. Otter	0.63 ± 0.093	0.79 ± 0.075	0.96 ± 0.166
Igri	-	0.78 ± 0.044	1.24 ± 0.275
Video	0.83 ± 0.110	-	-

Confidence limits at $P = 0.05$

TABLE 3.6.2c: Rate of whole plant tiller emergence per mainstem leaf

Variety	S81	S821	S822
Gerbel	-	1.06 ± 0.118	1.13 ± 0.969
Athene	1.01 ± 0.195	1.10 ± 0.200	0.87 ± 0.381
M. Otter	0.95 ± 0.261	1.10 ± 0.106	1.46 ± 0.794
Igri	-	0.94 ± 0.165	1.09 ± 0.159
Video	1.20 ± 0.096	-	-
Sowing date mean (fitted separately)	1.08 ± 0.080	1.08 ± 0.061	1.06 ± 0.133

Confidence limits at $P = 0.05$

TABLE 3.6.2d: Number of leaves unfolded at GS21 from the regression equation for Table 3.6.2c (observed values shown in brackets)

Variety	S81	S821	S822
Gerbel		2.9 (3.0)	2.9 (3.0)
Athene	1.6 (2.0)	2.5 (3.0)	3.4 (3.5)
M. Otter	1.4 (2.0)	2.7 (3.0)	3.5 (3.5)
Igri	-	2.6 (3.0)	2.8 (3.0)
Video	1.6 (2.0)	-	-
Sowing date mean	1.6 ± 0.38	2.7 ± 0.31	3.2 ± 0.62

TABLE 3.6.2e: Maximum number of tillers per plant

Variety	S81	S821	S822
Gerbel	-	4.0	3.3
Athene	6.1	4.1	3.1
M. Otter	6.8	4.9	4.1
Igri	-	4.4	4.2
Video	8.4	-	-
Sowing date mean	7.1	4.3	3.7
s.e. of mean (9 d.f. in S81, 21 d.f. in S82)	1.36	0.99	0.99
L.S.D. for treatment mean (P = 0.05)	2.14	1.44	1.44

TABLE 3.6.3: Final number of ear-bearing tillers per plant

Variety	Number of tillers per plant			Percentage survival from the maximum tiller number		
	S81	S821	S822	S81	S821	S822
Gerbel	-	0.14	0.26	-	4	8
Athene	1.89	0.05	0.22	31	1	7
M. Otter	5.14	1.36	2.10	76	28	51
Igri	-	0.78	1.14	-	18	21
Video	6.12	-	-	73	-	-

The two-row varieties did not exhibit similar tiller abortion after mainstem anthesis, and in S82 they produced late tillers after a wet period in mid-June. These late tillers did not contribute to grain yield though some had reached ear emergence by the time of the final harvest. In S822 Maris Otter had 0.25 green ears per plant at the final harvest as well as other late tillers without emerged ears.

The differences between the six-row and two-row types, in the number of ears per plant, and the production of late tillers in the two-row varieties, gave more even crop ripening in the six-row cultivars. This is demonstrated by the difference between Athene and Maris Otter in the duration of ear emergence and anthesis in the whole crop (Fig. 3.6.3).

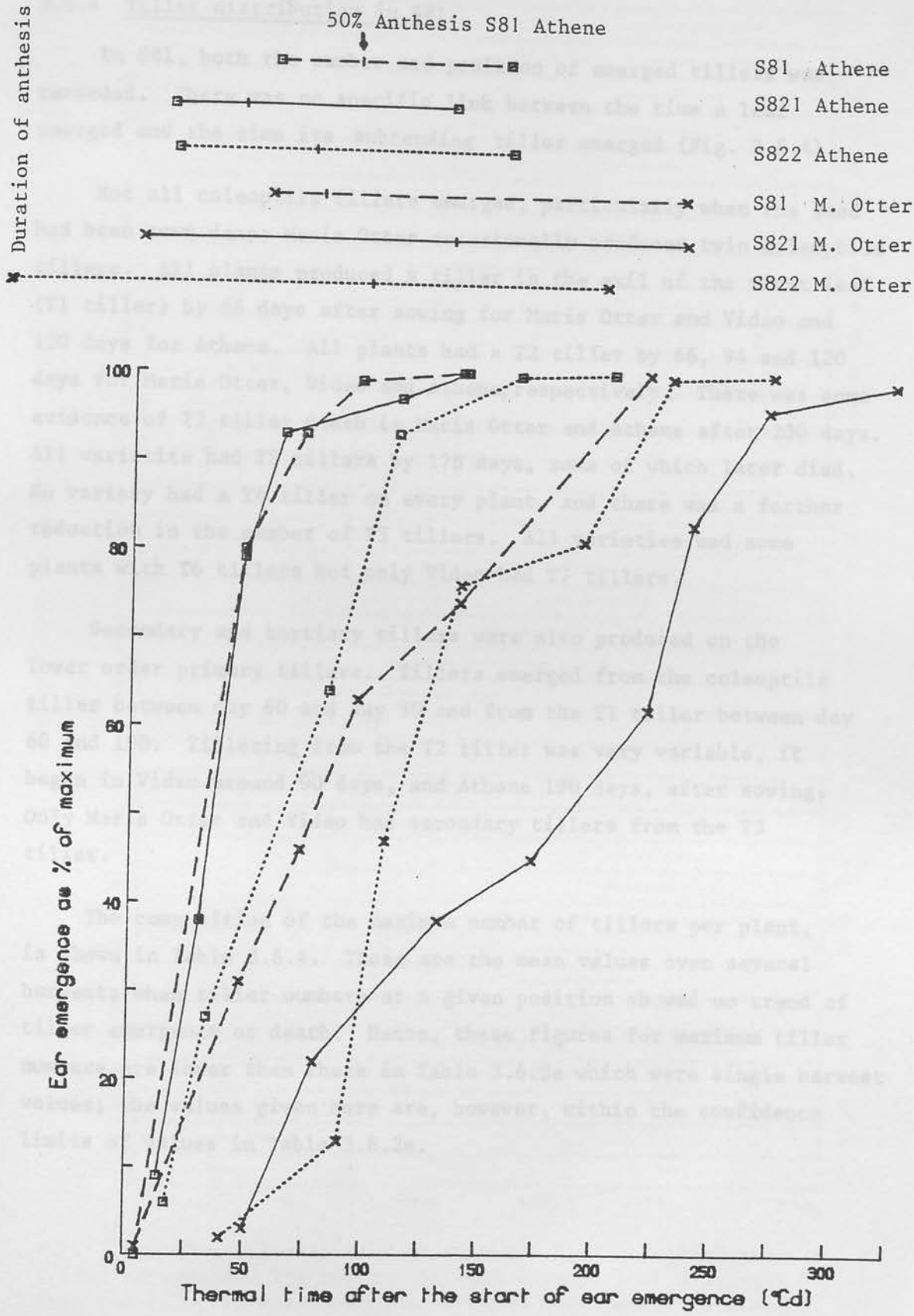

Fig. 3.6.3 Duration of ear emergence and anthesis for Athene and Maris Otter.

3.6.4 Tiller distribution in S81

In S81, both the number and position of emerged tillers was recorded. There was no specific link between the time a leaf emerged and the time its subtending tiller emerged (Fig. 3.6.4).

Not all coleoptile tillers emerged, particularly when the seed had been sown deep; Maris Otter occasionally produced twin coleoptile tillers. All plants produced a tiller in the axil of the first leaf (T1 tiller) by 66 days after sowing for Maris Otter and Video and 120 days for Athene. All plants had a T2 tiller by 66, 94 and 120 days for Maris Otter, Video and Athene, respectively. There was some evidence of T2 tiller death in Maris Otter and Athene after 230 days. All varieties had T3 tillers by 178 days, some of which later died. No variety had a T4 tiller on every plant, and there was a further reduction in the number of T5 tillers. All varieties had some plants with T6 tillers but only Video had T7 tillers.

Secondary and tertiary tillers were also produced on the lower order primary tillers. Tillers emerged from the coleoptile tiller between day 60 and day 90 and from the T1 tiller between day 60 and 150. Tillering from the T2 tiller was very variable, it began in Video around 90 days, and Athene 190 days, after sowing. Only Maris Otter and Video had secondary tillers from the T3 tiller.

The composition of the maximum number of tillers per plant, is shown in Table 3.6.4. These are the mean values over several harvests when tiller numbers at a given position showed no trend of tiller emergence or death. Hence, these figures for maximum tiller numbers are lower than those in Table 3.6.2e which were single harvest values; the values given here are, however, within the confidence limits of values in Table 3.6.2e.

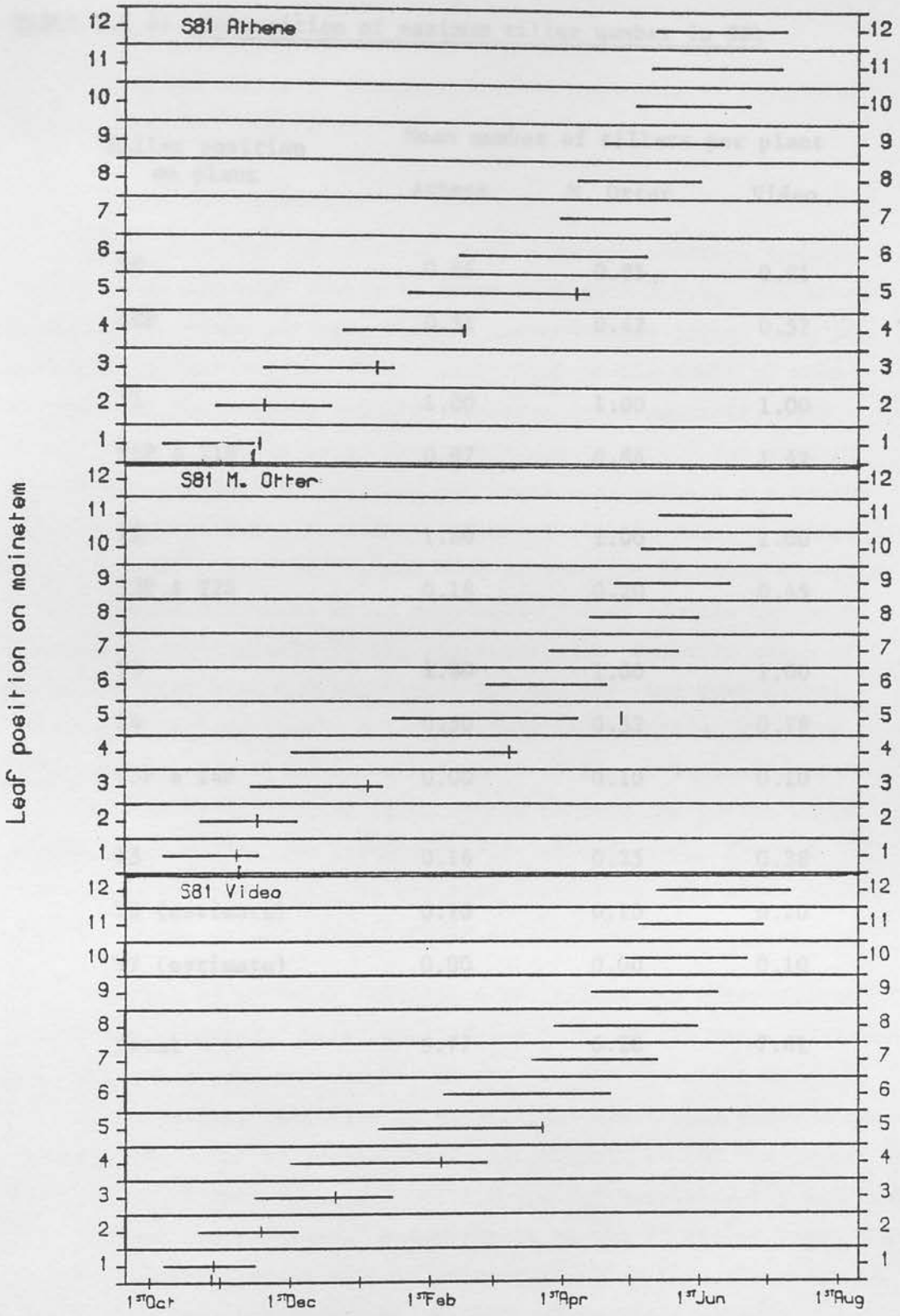

Fig. 3.6.4 The relation between mainstem leaf unfolding and tiller emergence. The horizontal line denotes leaf longevity from unfolding to death and the vertical line marks the time when 50% of plants had a tiller emerged from the axil of that leaf (except for the T5 marker which denotes the maximum number of T5 tillers; T5 emerged from less than 50% of plants).

TABLE 3.6.4: Composition of maximum tiller number in S81

Tiller position on plant	Mean number of tillers per plant		
	Athene	M. Otter	Video
TC	0.65	0.85	0.81
TCP	0.31	0.42	0.57
T1	1.00	1.00	1.00
T1P & T1S	0.87	0.84	1.42
T2	1.00	1.00	1.00
T2P & T2S	0.18	0.20	0.45
T3	1.00	1.00	1.00
T4	0.50	0.52	0.78
T3P & T4P	0.00	0.10	0.10
T5	0.16	0.25	0.38
T6 (estimate)	0.10	0.10	0.20
T7 (estimate)	0.00	0.00	0.10
Total	5.77	6.28	7.81

3.7 Number of Grains per Ear

All measurements in Sections 3.7 and 3.8 refer to mainstems unless otherwise specified.

3.7.1 Spikelet initiation

The progression of spikelet initiation and abortion against thermal time for each sowing is shown in Figure 3.7.1. All treatments had a common pattern, with an approximately linear rate of spikelet production from floral initiation to the start of stem elongation, followed by spikelet abortion until anthesis, with further loss of grain sites due to sterile florets. The greater number of spikelets for six-row cultivars was entirely due to the lateral florets being fertile. The change in the rate of primordia production at floral initiation (see Section 3.1.4) often occurred after several primordia which eventually formed florets had been initiated, particularly in the early sowings. Separate rates of spikelet initiation were calculated for the pre- and post-floral initiation periods (Table 3.7.1a). Pre-floral initiation rates could not be calculated in some treatments due to lack of data. The post-floral initiation rates do not include the period close to the maximum when the initiation rate slowed down. Where a comparison was possible, the spikelet initiation rate after floral initiation was always significantly greater than that before.

The rate of spikelet initiation per degree day after floral initiation, increased with later sowing. Though the rates of spikelet initiation were much higher in the six-row varieties than the two-row varieties, there was no significant difference between the types in the rate of rachis level initiation. In S81 the spikelet initiation rate for the T1 tiller was not significantly different from that on the mainstem. Measurements on the T1 tiller began when it had 15 rachis levels already present at which time the mainstem had 18 (M. Otter and Video) or 19 (Athene) rachis levels.

Faster rates of spikelet initiation in later sowings, were coupled with a shorter duration of initiation (Table 3.7.1b). The six-row cultivars produced a similar number of rachis levels to the two-row varieties, except in S81 when Athene had significantly fewer rachis levels than Maris Otter or Video (Table 3.7.1c).

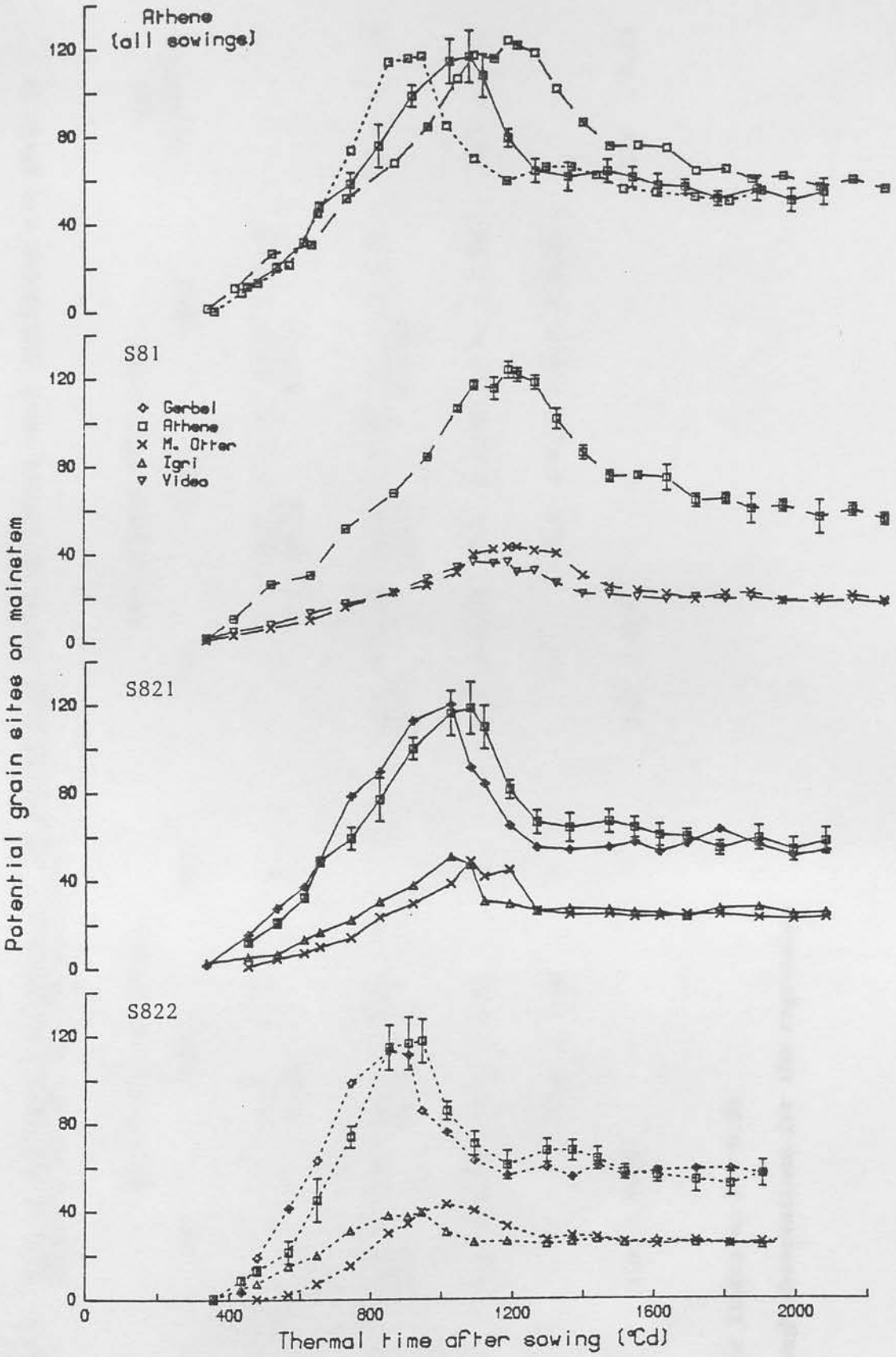

Fig 3.7.1 Change in number of potential grain sites with thermal time.

TABLE 3.7.1a: Rate of spikelet initiation per 100 degree days (rates of rachis level initiation are given in brackets for the six-row cultivars)

	Pre-floral initiation			Post-floral initiation			S81 T1 tiller
	S81	S821	S822	S81	S821	S822	
Gerbel	-	12.9 ± 0.93 (4.3)	*	-	20.5 ± 2.90 (6.8)	27.2 ± 2.13 (9.1)	-
Athene	10.4 ± 3.97 (3.5)	12.7 ± 6.95 (4.2)	10.1 ± 0.70 (3.4)	17.2 ± 1.07 (5.7)	19.8 ± 1.40 (6.6)	32.8 ± 3.33 (10.9)	17.8 ± 1.58
M. Otter	3.2 ± 0.23	3.8 ± 1.93	*	6.2 ± 0.70	8.4 ± 0.73	10.4 ± 0.90	6.2 ± 1.42
Igri	-	1.9 ± 1.08	*	-	8.6 ± 0.49	8.2 ± 0.51	-
Video	3.4 ± 1.78	-	-	5.2 ± 0.41	-	-	6.1 ± 0.72

Confidence limits at $P = 0.05$

* Not enough observations for the regression

TABLE 3.7.1b: Duration of spikelet initiation

Variety	Thermal time (^{o}Cd) from collar initiation to maximum primordia number		
	S81	S821	S822
Gerbel	-	720	520
Athene	890	770	600
M. Otter	890	700	550
Igri	-	750	640
Video	870	-	-

TABLE 3.7.1c: Maximum number of potentially fertile spikelet primordia (number of rachis levels given in brackets for the six-row cultivars)

Variety	S81	S821	S822	S81 T1 tiller
Gerbel	-	120 (40)	114 (38)	-
Athene	126 (42)	118 (39)	118 (39)	117 (39)
M. Otter	45	48	43	43
Igri	-	50	40	-
Video	38	-	-	36
s.e. of mean	3.5	4.9	4.2	2.4
d.f.	9	21	21	9
L.S.D. for treatment mean (P = 0.05)	5.4	7.6	6.6	3.8

3.7.2 Spikelet abortion

The period of spikelet abortion, from the time of maximum spikelet number to anthesis, coincided with high relative growth rates for the whole plant (Fig. 3.7.2). Between 35 and 55 per cent of spikelets were lost in this period, the greatest loss being in S821 (Table 3.7.2a).

There was no relationship between the apical development stage at which a spikelet was initiated and its likely survival. For example, the last surviving floret was initiated at the start of the triple mound stage in S81 Maris Otter, and at the stamen initial stage in S821 Maris Otter.

Florets on the first and second rachis levels above the collar were often small and infertile, but since they were not aborted they were only counted as dead once anthesis was complete. Various other florets at higher positions on the ear did not fertilise; the incidence of these 'sterile florets' further reduced the final number of grains per ear (Table 3.7.2b).

A comparison of the number of grains per mainstem ear (Table 3.7.2c) with the whole crop grains per unit area (see Table 3.9.2) shows that the samples chosen for mainstem observation were biased towards large ears. This error was caused by the difficulty in separating plants, and distinguishing mainstems, during stem elongation and must have led to an over-estimate of the real rate of spikelet survival.

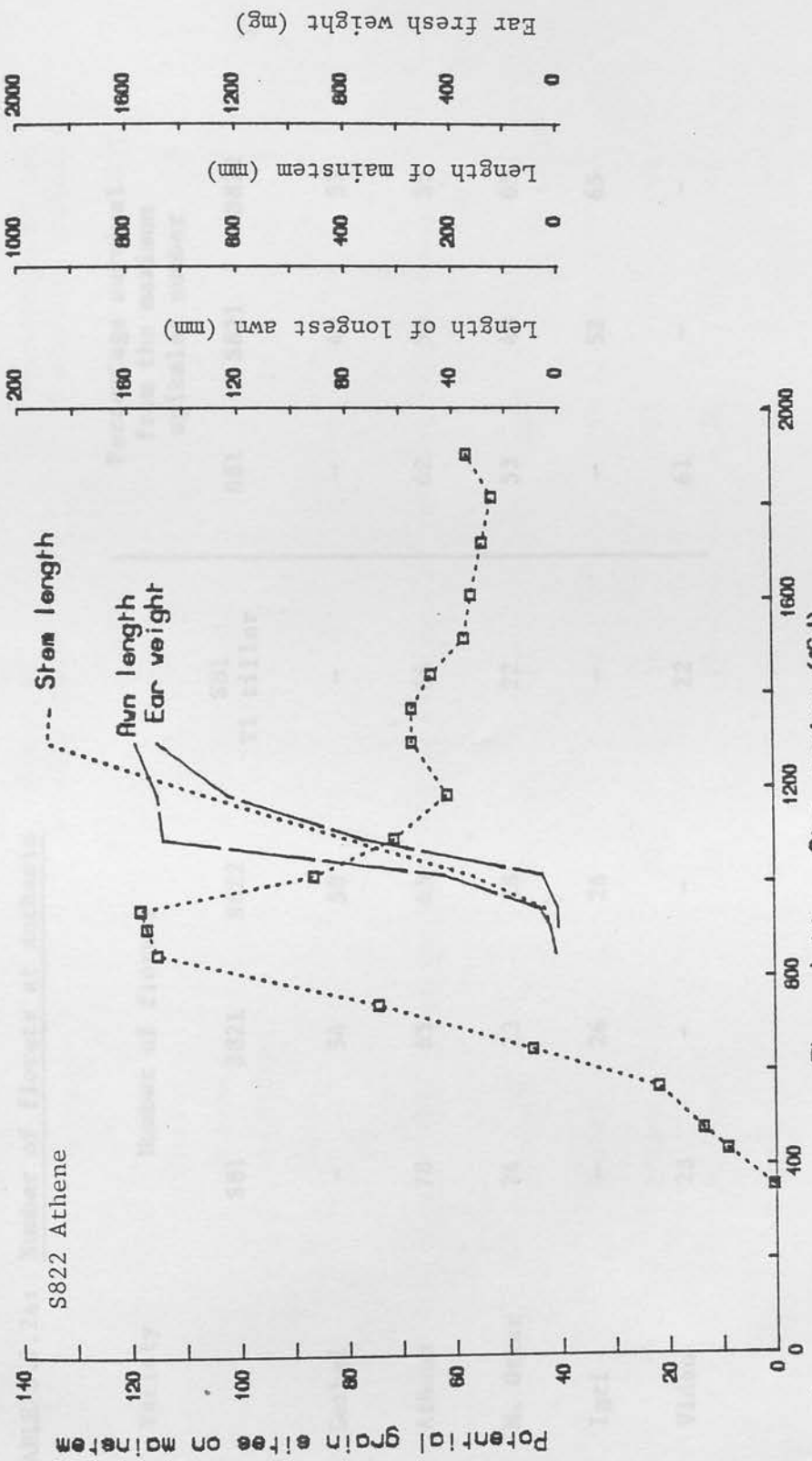

Fig. 3.7.2 The relation between spikelet abortion and plant growth.

TABLE 3.7.2a: Number of florets at anthesis

Variety	Number of florets				Percentage survival from the maximum spikelet number			
	S81	S821	S822	S81 T1 tiller	S81	S821	S822	S81 T1 tiller
Gerbel	-	54	58	-	-	45	51	-
Athene	78	65	65	66	62	55	55	56
M. Otter	24	23	28	22	53	48	65	51
Igri	-	26	26	-	-	52	65	-
Video	23	-	-	22	61	-	-	61

TABLE 3.7.2b: Number of sterile florets on the mainstem ear (not recorded in S81)

Variety	Number of sterile florets		Percentage of the florets at anthesis	
	S821	S822	S821	S822
Gerbel	5	5	9	8
Athene	12	13	18	19
M. Otter	3	2	12	7
Igri	1	2	4	7

TABLE 3.7.2c: Final number of grains per mainstem ear (mean of the last three harvests)

Variety	S81	S821	S822	S81 T1 tiller
Gerbel	-	52	59	-
Athene	60	56	55	50
M. Otter	22	21	26	19
Igri	-	24	25	-
Video	20	-	-	19

3.8 Grain Size

3.8.1 Spikelet size

In the S82 sowings the volume of the ear was measured once the collar was visible. Ear fresh weight was recorded from the time of apical tip death, and grain dry weight recorded after anthesis. In order to have a direct comparison between the six and two-row types, the ear size per viable spikelet/grain was calculated.

The increase in ear size per spikelet in all varieties followed a similar pattern to that shown by S821 Igri and Athene (Fig. 3.8.1a). The ear fresh weight growth rate slowed down considerably around anthesis before resuming growth in grain filling. The log plot of these varieties shows that the increase in ear volume per spikelet before tip death, and ear fresh weight per spikelet to anthesis, was exponential (Fig. 3.8.1b). The change in the rate of increase of ear volume per spikelet around the time of tip death was probably due to the death of the smallest spikelets after this stage, though there was a change in the method of calculating ear volume at this time (Section 2.2.2).

Differences between treatments in the relative growth rate of ear volume per spikelet, and ear fresh weight per spikelet, were difficult to establish, due to the small number of observations made in the relevant period (Table 3.8.1a). There were important differences in the duration of the growth phase, especially from tip death to the start of anthesis (Table 3.8.1b). With a relative growth rate per degree day of 0.02; spikelet fresh weight would double in 50°Cd (about 7 days).

TABLE 3.8.1a: Spikelet relative growth rate per 100 degree days (not recorded in S81)

Variety	Ear volume per spikelet RGR during spikelet initiation				Ear fresh weight per spikelet RGR from tip death to anthesis			
	S821		S822		S821		S822	
Gerbel	1.27	± 0.167	1.28	± 0.163	2.2	± 0.63	2.7	± 0.28
Athene	1.57	± 0.132	1.42	± 0.268	2.8	± 0.44	2.2	± 1.01
M. Otter	1.03	± 0.313	1.83	± 0.411	2.2	± 0.74	1.7	± 0.29
Igri	1.14	± 0.092	1.16	± 0.119	2.2	± 0.88	3.2	± 0.98

Confidence limits at $P = 0.05$

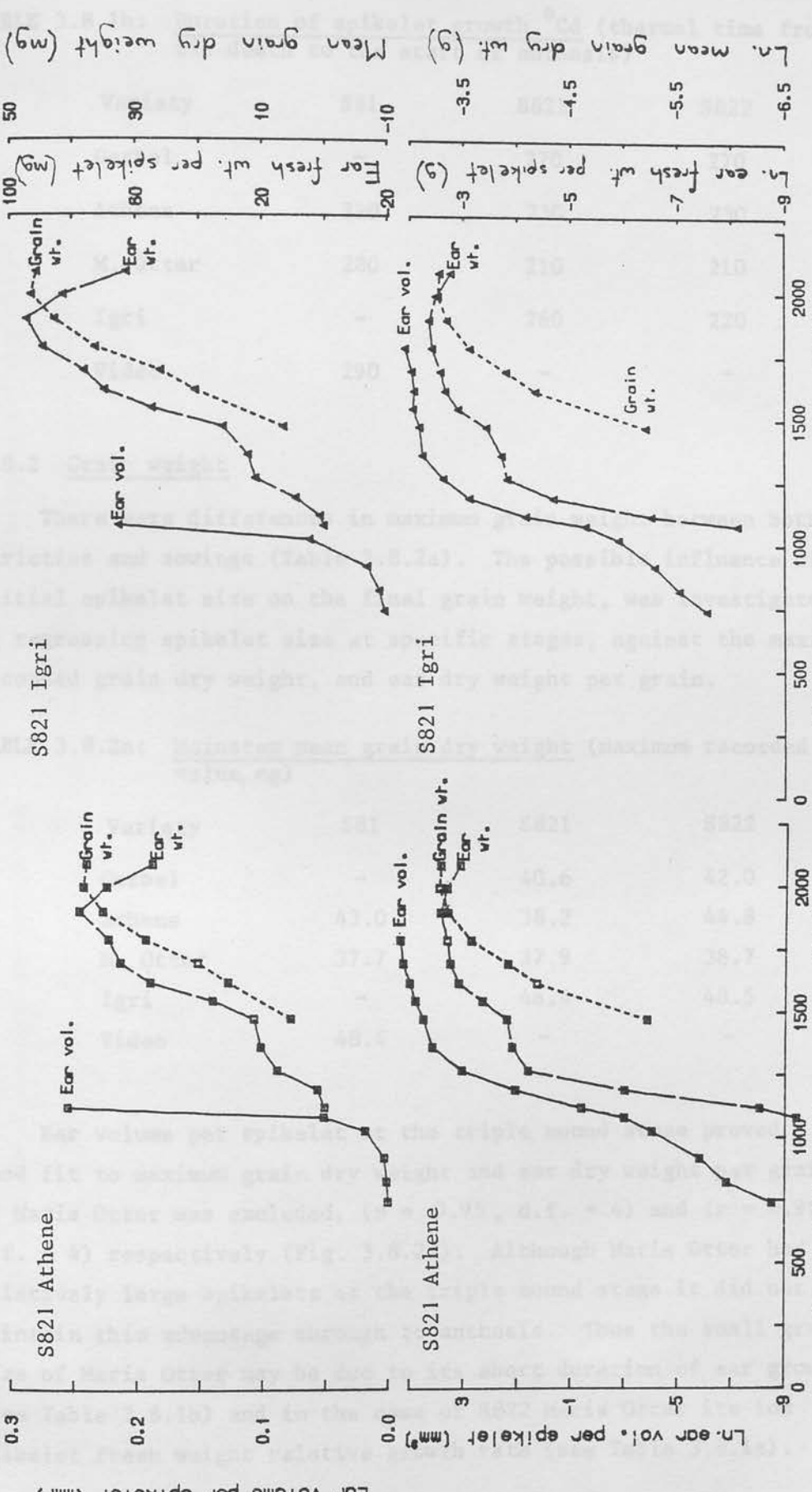

Fig. 3.8.1 a The increase in ear size per spikelet with thermal time.

Fig 3.8.1 b The increase in log, ear size per spikelet with thermal time.

TABLE 3.8.1b: Duration of spikelet growth °Cd (thermal time from tip death to the start of anthesis)

Variety	S81	S821	S822
Gerbel	-	270	270
Athene	320	230	230
M. Otter	280	210	210
Igri	-	260	220
Video	290	-	-

3.8.2 Grain weight

There were differences in maximum grain weight between both varieties and sowings (Table 3.8.2a). The possible influence of initial spikelet size on the final grain weight, was investigated by regressing spikelet size at specific stages, against the maximum recorded grain dry weight, and ear dry weight per grain.

TABLE 3.8.2a: Mainstem mean grain dry weight (maximum recorded value, mg)

Variety	S81	S821	S822
Gerbel	-	40.6	42.0
Athene	43.0	38.2	44.8
M. Otter	37.7	37.9	38.7
Igri	-	46.4	48.5
Video	48.4	-	-

Ear volume per spikelet at the triple mound stage proved a good fit to maximum grain dry weight and ear dry weight per grain if Maris Otter was excluded, (r = 0.95, d.f. = 4) and (r = 0.92, d.f. = 4) respectively (Fig. 3.8.2a). Although Maris Otter had relatively large spikelets at the triple mound stage it did not maintain this advantage through to anthesis. Thus the small grain size of Maris Otter may be due to its short duration of ear growth (see Table 3.8.1b) and in the case of S822 Maris Otter its low spikelet fresh weight relative growth rate (see Table 3.8.1a).

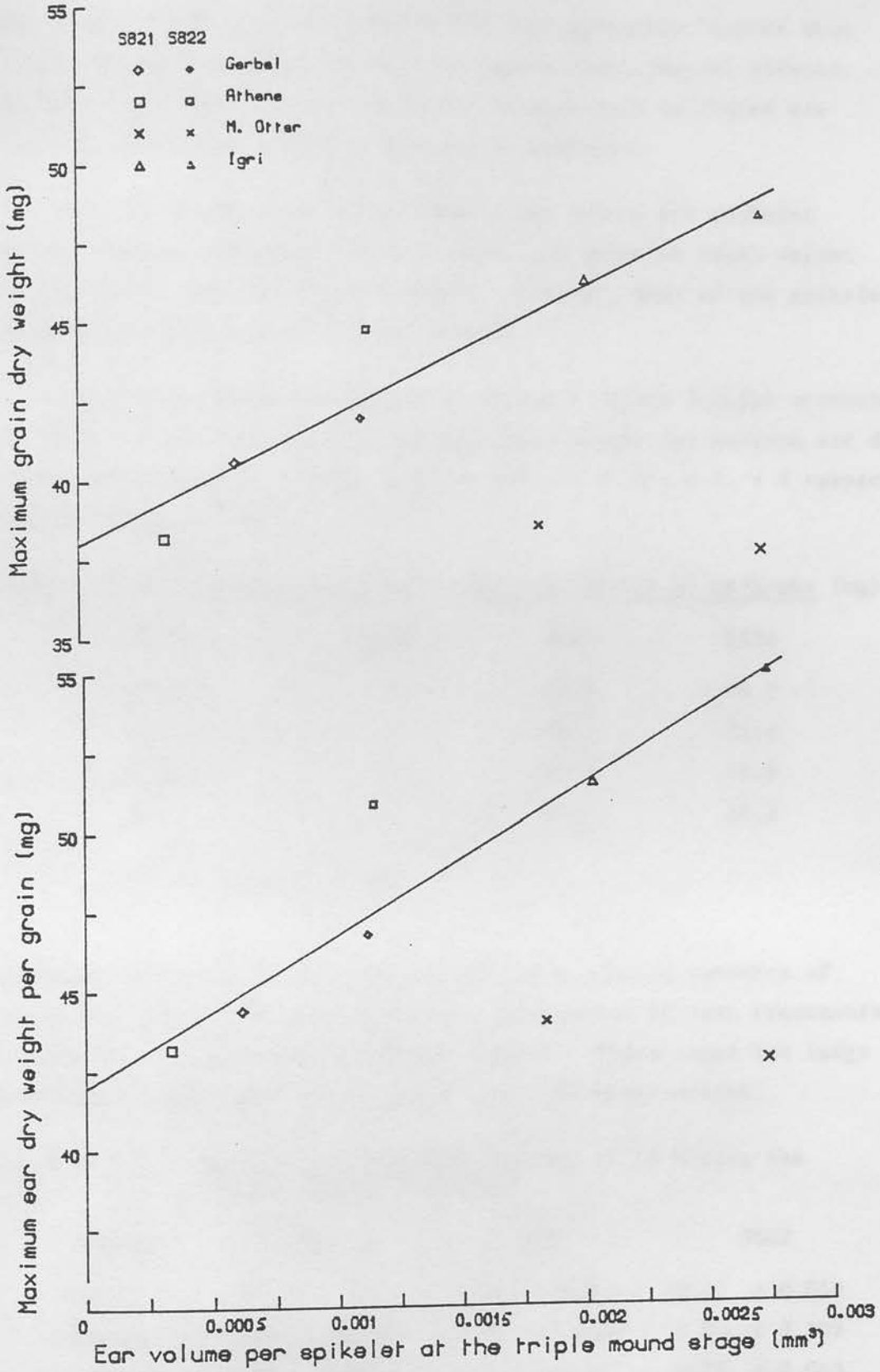

Fig 3.8.2 a The relation between maximum grain dry weight and ear volume per spikelet at the triple mound stage. The fitted lines exclude Maris Otter;
for maximum grain dry weight $y = 38(\pm 1.4) + 4000(\pm 920)x$;
for maximum ear dry weight per grain $y = 42(\pm 1.9) + 4800(\pm 1230)x$.

The triple mound stage was chosen for the regression, rather than a certain date or time, in order to remove developmental effects. At the triple mound stage the number of spikelets initiated was close to the final number of florets at anthesis.

No relationship was found between ear volume per spikelet at the time of maximum primordia number (or spikelet fresh weight at tip death) and final grain weight. However, many of the spikelets present at this time were later aborted.

Ear fresh weight per floret at anthesis (Table 3.8.2b) accounted for most of the variation in maximum grain weight and maximum ear dry weight per grain, (r = 0.93, d.f.= 6 and r = 0.95 , d.f. = 6 respectively) (Fig. 3.8.2b).

TABLE 3.8.2b: Mainstem ear fresh weight per floret at anthesis (mg)

Variety	S81*	S821	S822
Gerbel	-	18.3	19.2
Athene	*	19.2	22.4
M. Otter	*	15.0	16.6
Igri	-	24.7	30.2

* Not recorded in S81

Although varieties in all sowings exhibited similar patterns of grain fill (Fig. 3.8.2c), there were differences between treatments in the rate of grain growth (Table 3.8.2c). These rates had large confidence limits due to the small number of observations.

TABLE 3.8.2c: Rate of grain growth (mg per 10^{o}Cd during the linear period of growth)

Variety	S81	S821	S822
Gerbel	-	0.75 ± 0.061	0.77 ± 0.059
Athene	0.70 ± 0.053	0.71 ± 0.034	0.88 ± 0.109
M. Otter	0.79 ± 0.067	0.76 ± 0.071	0.76 ± 0.065
Igri	-	0.87 ± 0.072	0.94 ± 0.081
Video	1.00 ± 0.145	-	-

Confidence limits at P = 0.05

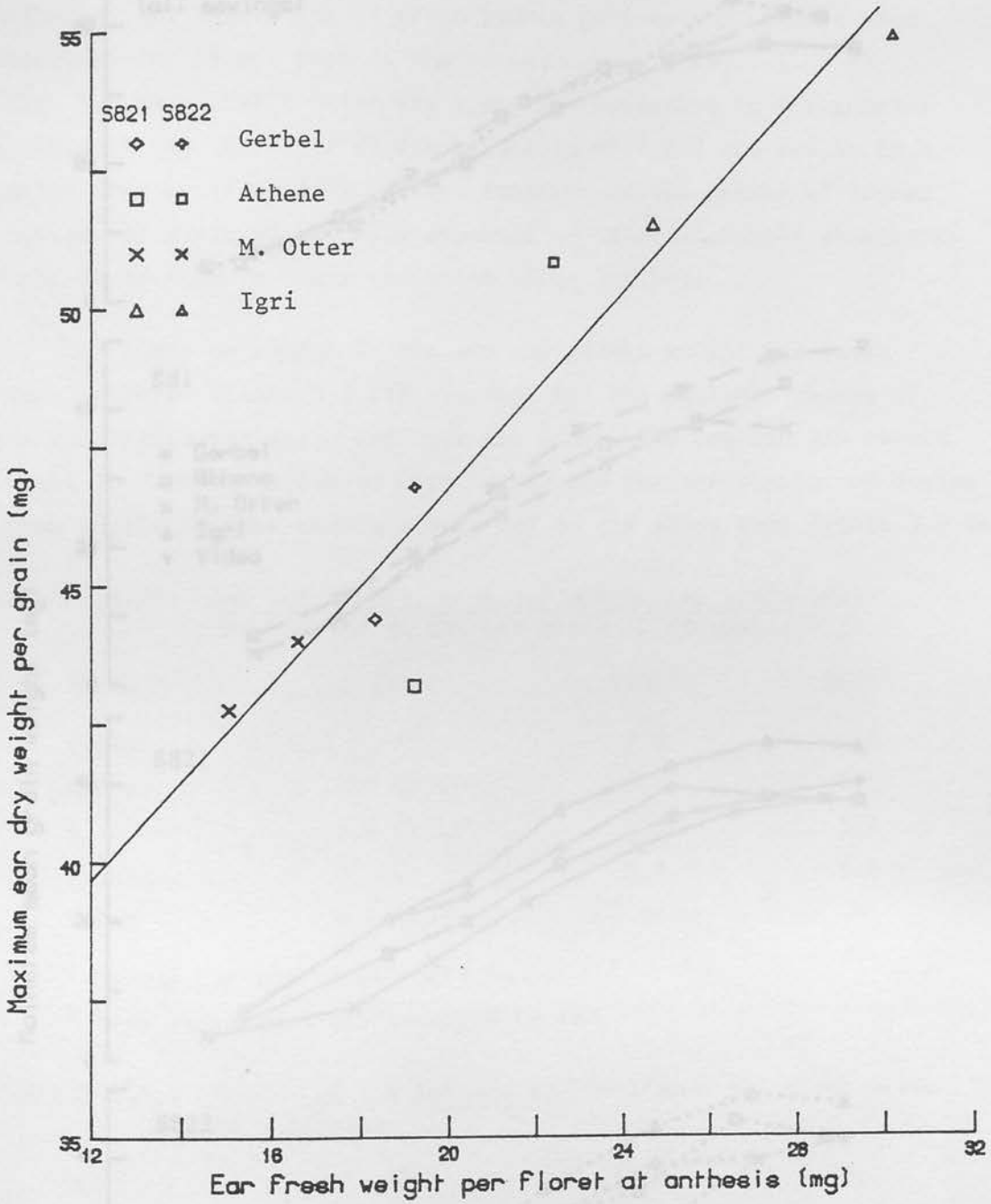

Fig. 3.8.2 b The relation between maximum ear dry weight per grain and ear fresh weight per floret at anthesis.
Fitted line : $y = 29(\pm 3.1) + 0.89(\pm 0.147)x$.

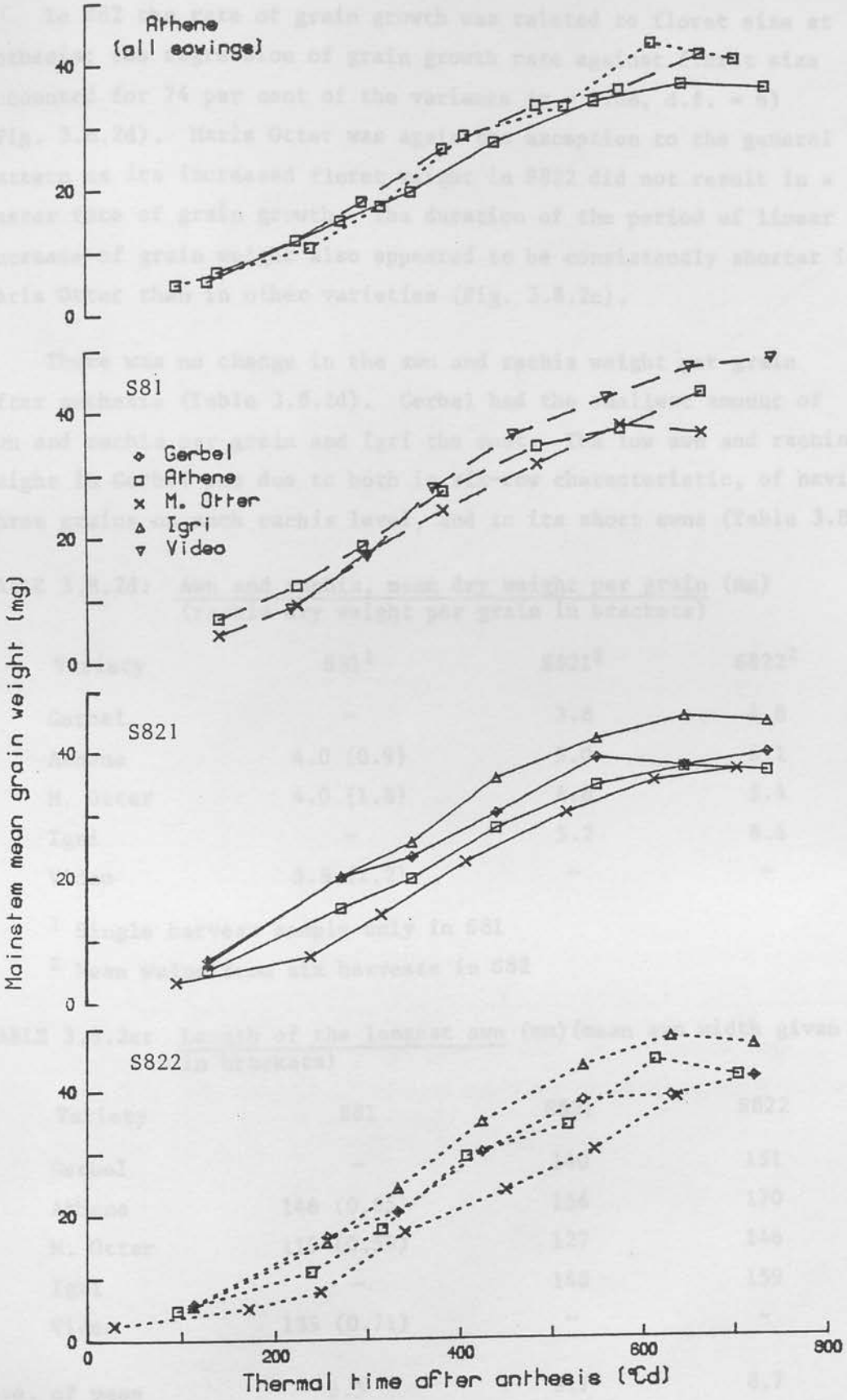

Fig. 3.8.2 c The increase in the mainstem mean grain weight after anthesis.

In S82 the rate of grain growth was related to floret size at anthesis; the regression of grain growth rate against floret size accounted for 74 per cent of the variance (r = 0.88, d.f. = 6) (Fig. 3.8.2d). Maris Otter was again the exception to the general pattern as its increased floret weight in S822 did not result in a faster rate of grain growth. The duration of the period of linear increase of grain weight also appeared to be consistently shorter in Maris Otter than in other varieties (Fig. 3.8.2c).

There was no change in the awn and rachis weight per grain after anthesis (Table 3.8.2d). Gerbel had the smallest amount of awn and rachis per grain and Igri the most. The low awn and rachis weight in Gerbel was due to both is six-row characteristic, of having three grains on each rachis level, and to its short awns (Table 3.8.2e).

TABLE 3.8.2d: Awn and rachis, mean dry weight per grain (mg) (rachis dry weight per grain in brackets)

Variety	S81[1]	S821[2]	S822[2]
Gerbel	-	3.8	4.8
Athene	4.0 (0.9)	5.0	6.1
M. Otter	4.0 (1.8)	4.8	5.4
Igri	-	5.2	6.6
Video	5.8 (2.2)	-	-

[1] Single harvest sample only in S81

[2] Mean value from six harvests in S82

TABLE 3.8.2e: Length of the longest awn (mm) (mean awn width given in brackets)

Variety	S81	S821	S822
Gerbel	-	140	151
Athene	146 (0.65)	156	170
M. Otter	119 (0.59)	127	146
Igri	-	148	159
Video	135 (0.71)	-	-
s.e. of mean	9.5	8.7	8.7
d.f.	9	21	21
L.S.D. for treatment mean (P = 0.05)	15.0	12.7	12.7

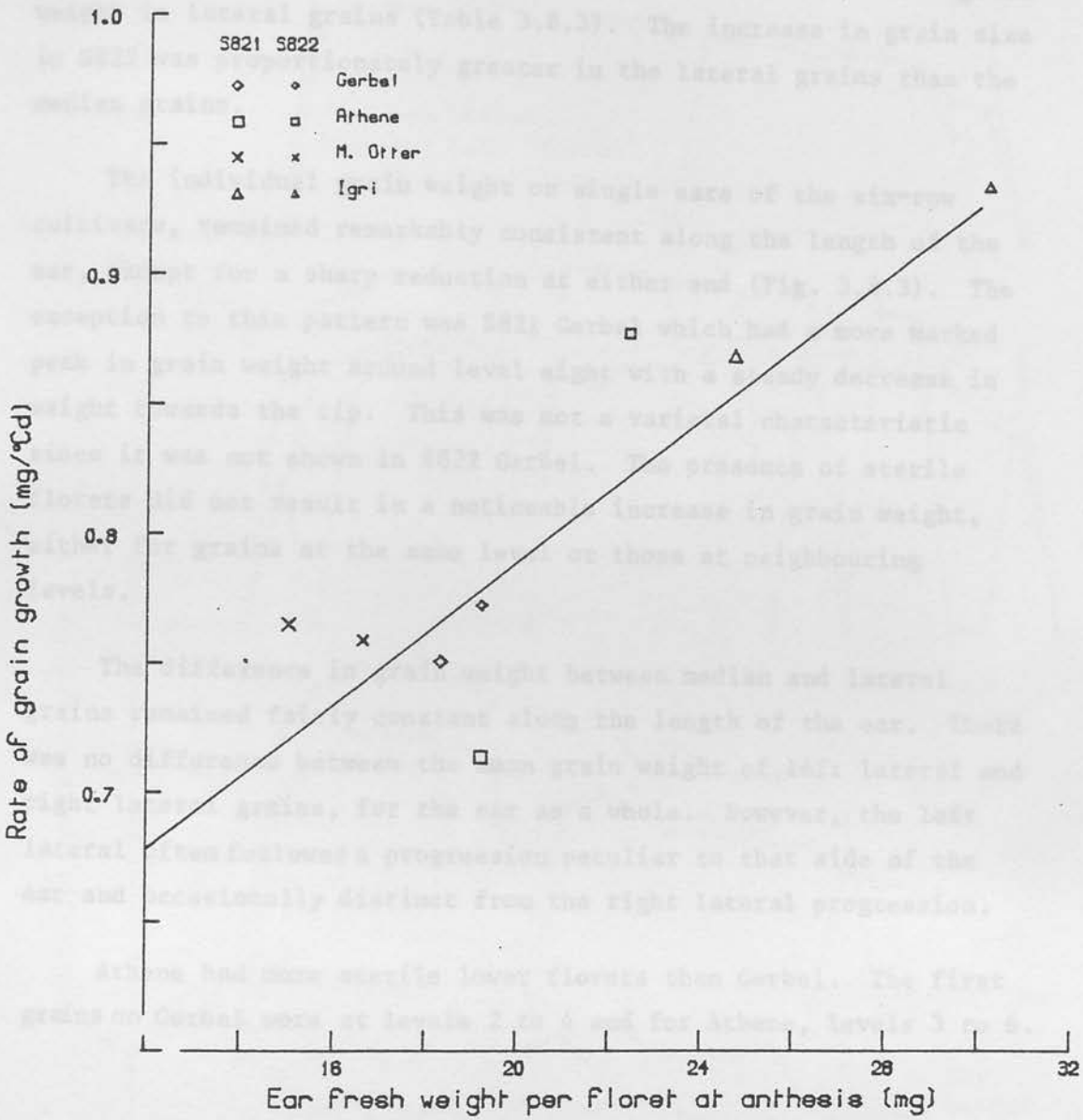

Fig. 3.8.2 d The relation between the rate of grain growth and ear fresh weight per floret at anthesis.
Fitted line : $y = 0.51(\pm 0.068) + 0.014(\pm 0.0035)x$.

3.8.3 Median and lateral grain size

Both Gerbel and Athene had a similar proportion of their grain weight in lateral grains (Table 3.8.3). The increase in grain size in S822 was proportionately greater in the lateral grains than the median grains.

The individual grain weight on single ears of the six-row cultivars, remained remarkably consistent along the length of the ear, except for a sharp reduction at either end (Fig. 3.8.3). The exception to this pattern was S821 Gerbel which had a more marked peak in grain weight around level eight with a steady decrease in weight towards the tip. This was not a varietal characteristic since it was not shown in S822 Gerbel. The presence of sterile florets did not result in a noticeable increase in grain weight, either for grains at the same level or those at neighbouring levels.

The difference in grain weight between median and lateral grains remained fairly constant along the length of the ear. There was no difference between the mean grain weight of left lateral and right lateral grains, for the ear as a whole. However, the left lateral often followed a progression peculiar to that side of the ear and occasionally distinct from the right lateral progression.

Athene had more sterile lower florets than Gerbel. The first grains on Gerbel were at levels 2 to 4 and for Athene, levels 3 to 6.

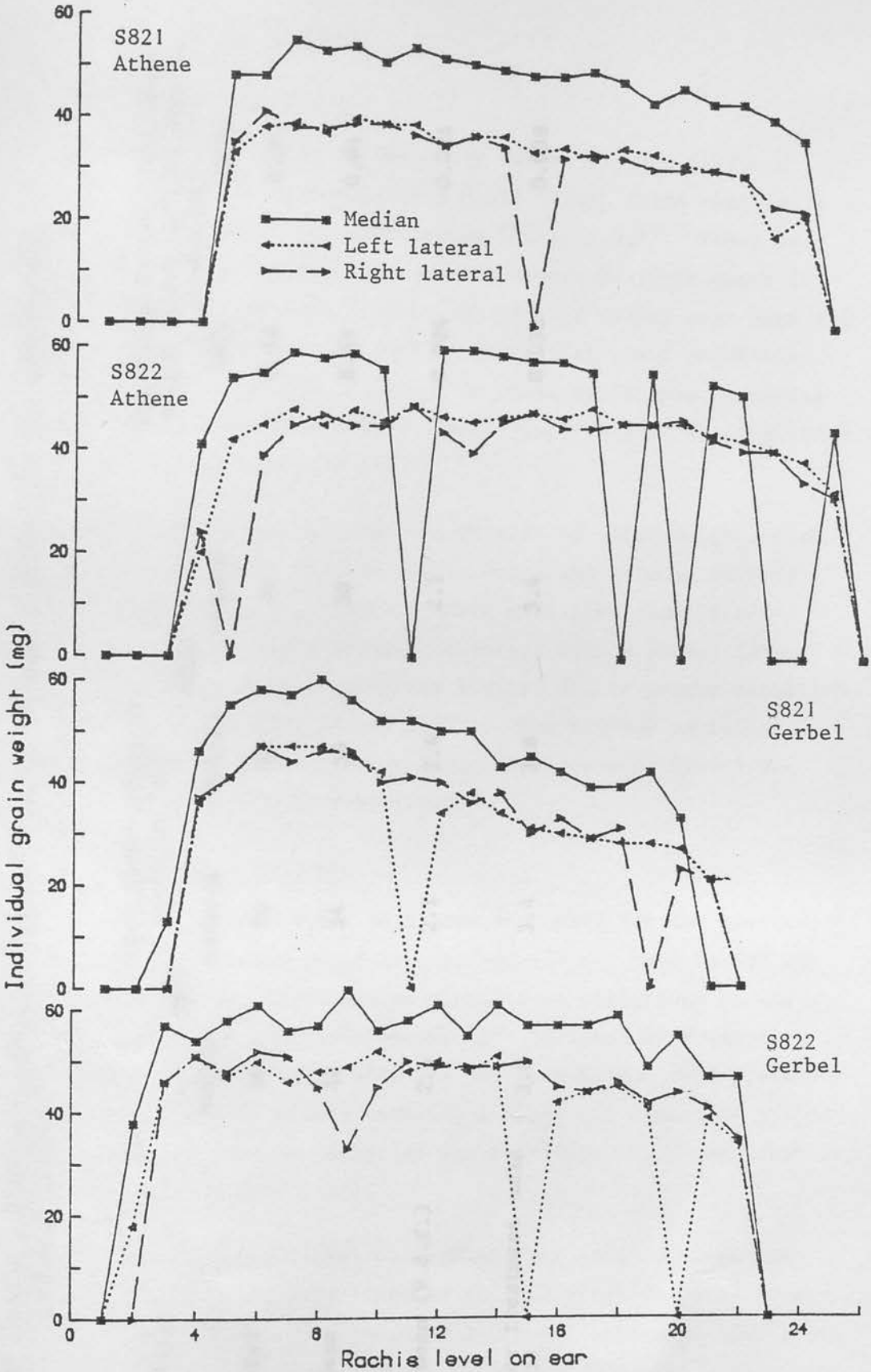

Fig. 3.8.3 The relation between grain weight and its position on the ear. Individual grain weight on single ears of the six row cultivars chosen at random.

TABLE 3.8.3: Median and lateral grain size (results from 20 randomly selected ears for each six-row treatment in S82)

Variety	Mean grain weight at maturity (mg)				The proportion of total grain weight in the lateral grains at maturity	
	S821		S822			
	Median	Lateral	Median	Lateral	S821	S822
Gerbel	50	35	52	39	0.58	0.59
Athene	48	34	53	38	0.59	0.61
s.e. of mean (9 d.f.)	2.4	2.1	2.4	2.1	0.024	0.024
L.S.D. for treatment mean (P = 0.05)	3.8	3.4	3.8	3.4	0.038	0.038

3.9 Final Yield Partitioning

3.9.1 Dry matter partioning

Within each sowing date, shoot dry weight did not differ significantly between varieties ($P \leq 0.05$) though large confidence limits may have hidden real differences (Table 3.9.1). There were significant differences in shoot weight between cultivar means in S82 and between sowing date means. S81 yielded 40 per cent more than the S82 mean despite having a much lower initial plant population (see Table 2.1a). In 1982, contrary to usual experience, delaying sowing by three weeks gave S822 a significantly higher shoot yield (10 per cent greater than S821).

Final grain yields followed the pattern of shoot weight, with significant differences between sowing dates and between variety means in S82 ($P \leq 0.01$). However, there were also significant differences in grain yield between varieties within sowing dates, except in S81 where large confidence limits, due to patchy establishment, mask any difference (Table 3.9.1). The six-row varieties generally had better grain yields than the two-row cultivars due largely to their higher harvest index.

3.9.2 Grain yield components

The number of grains per unit area accounted for the greatest overall variance in plot yield as expected (57 per cent in S82 and 56 per cent in S81). There was no significant difference in the number of grains per unit area between the S821 and S822 means, as the higher grain yield of S822 was due to a higher 1000 grain weight (Table 3.9.2). Within both S82 sowings the number of grains per unit area for six-row varieties was significantly higher than in any two-row variety ($P \leq 0.01$).

Regressing the individual plot grains per unit area against grain yield, gave regression lines of similar slope for each treatment, with the intercept displaced by different treatment 1000 grain weight (Fig. 3.9.2). Thousand grain weight was the most stable component of grain yield within each treatment. Within each sowing, differences in 1000 grain weight between varieties broadly reflect the cultivar's genetic potential. The only exception was the failure of S822 Maris Otter to increase its grain weight in line with other

TABLE 3.9.1: Final dry matter partitioning

	Shoot dry weight gm^{-2}	Ear dry weight gm^{-2}	Grain dry weight gm^{-2}	Harvest index
S81†				
Athene	1660	1010	880	0.53
M. Otter	1450	820	720	0.50
Video	1530	890	770	0.51
S81 mean	1550	910	790	0.52
S81 s.e. of mean (9 d.f.)	204	133	108	0.014
L.S.D. for treatment mean ($P = 0.05$)	ns	ns	ns	0.023
S821				
Gerbel	1120	700	640	0.57
Athene	1030	680	600	0.58
M. Otter	910	550	490	0.54
Igri	1080	670	600	0.56
S821 mean	1030	660	580	0.563
S822				
Gerbel	1190	800	720	0.60
Athene	1160	770	670	0.58
M. Otter	1100	620	540	0.49
Igri	1110	690	610	0.55
S822 mean	1140	720	630	0.555
S82 s.e. of mean (21 d.f.)	124	78	68	0.0115
L.S.D. for treatment mean ($P = 0.05$)	182	114	100	0.017

† S81 figures have been corrected to compensate for ears with bird damage.

varieties. This may have been caused by late tillering in S822 Maris Otter, or by harvesting this treatment before it had reached maximum grain yield. The different crop structure of the six-row and two-row cultivars is seen in the differences between the types in the number of ears per unit area and the number of grains per ear (Table 3.9.2).

An estimate of grains per ear counted on 30 ears chosen at random from each sample, gave close agreement with the number of grains per ear calculated from total yield, ears per unit area and 1000 grain weight. Only S822 Maris Otter had a counted value just outside the 95 per cent confidence limits for the calculated value (Table 3.9.2).

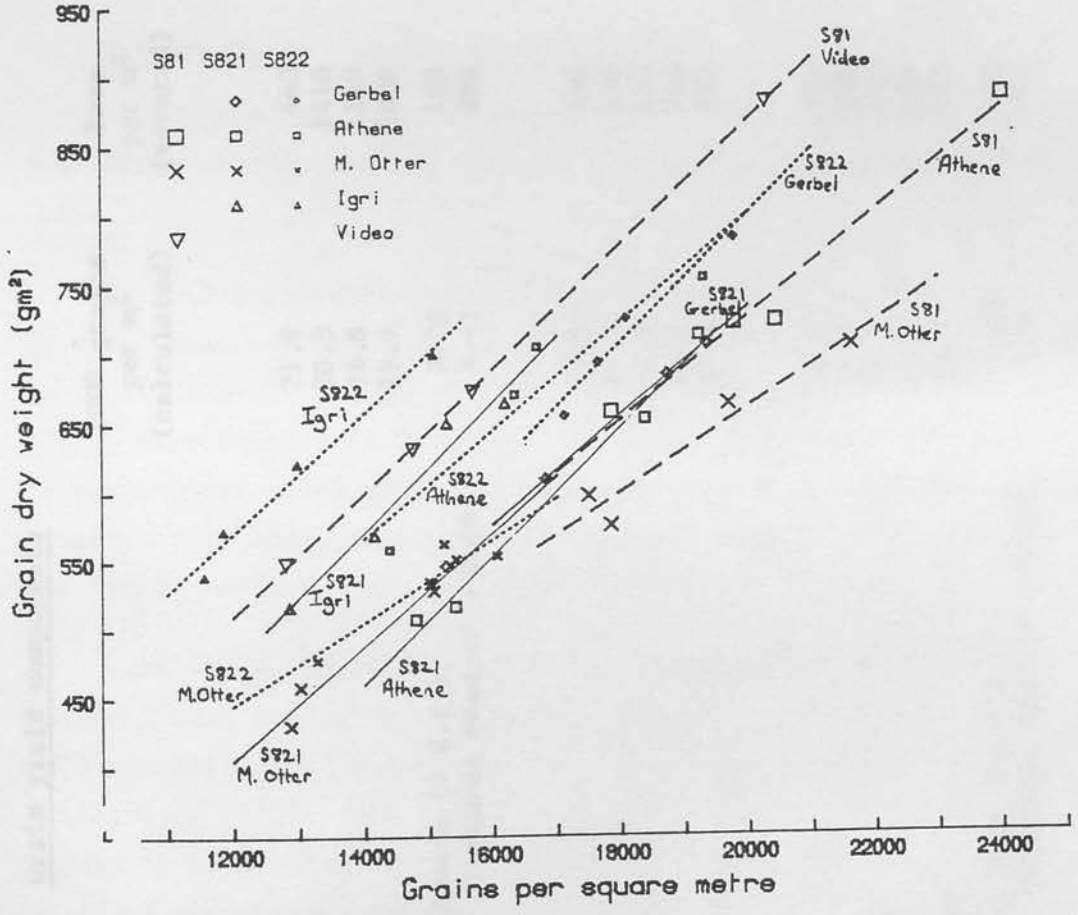

Fig 3.9.2 The relation between plot grain yield and the number of grains per square metre. Only M. Otter in S821 and S822 had a significantly different slope (P = 0.05) than other treatments.

TABLE 3.9.2: Grain yield components

	1000 grains per m^2 (calculated)	Ears per m^2 (counted)	Grains per ear (calculated)	Grains per ear (counted)	1000 grain dry weight (g)
S81					
Athene	21.9	460	47.3	-	36.5
M. Otter	20.3	1410	14.4	-	33.3
Video	16.8	1140	14.8	-	43.1
S81 mean	19.7	1000	25.5	-	37.6
S81 s.e. of mean (9 d.f.)	2.76	185	1.84	-	0.67
L.S.D. for treatment mean (P = 0.05)	4.42	296	2.96	-	1.08
S821					
Gerbel	17.5	430	40.5	41.1	36.4
Athene	17.0	410	41.4	43.0	35.2
M. Otter	14.0	920	15.2	15.8	34.9
Igri	14.7	740	19.8	19.1	41.1
S821 mean	15.8	630	29.2	29.7	36.9
S822					
Gerbel	18.1	420	43.6	41.9	39.4
Athene	16.6	400	41.4	40.9	40.4
M. Otter	15.1	870	17.4	19.4	35.8
Igri	12.9	660	19.4	21.2	47.4
S822 mean	15.7	590	30.5	30.8	40.7
S82 s.e. of mean (21 d.f.)	0.776	63	1.81	3.20	1.09
L.S.D. for treatment mean (P = 0.05)	1.14	93	2.66	4.70	1.60

CHAPTER IV

CROP DEVELOPMENT

Development in graminaceous plants is marked by changes at the stem apex. At the apex, ontogeny progresses through initiation of leaf primordia, floral initiation, and differentiation until anthesis. From the analysis of canopy development, dry matter production, and partitioning, it is evident that the only development stages marking the onset of different phases of growth, in winter barley are: seedling emergence, stem elongation (GS31), and anthesis. In a winter barley crop, both stem elongation and anthesis depend on the timing of floral initiation and the rate of floral development; factors which also influence the components of grain yield.

4.1 Environmental Control of Development

Development was best expressed in thermal, rather than calendar, time since plants perceive time as a function of temperature (Monteith, 1981).

Lack of assimilate supply can delay development, as well as plant growth. When expressed in thermal time, the initial rate of development (reciprocal of time to pass through development) of S822 was slower than other sowings. This effect was particularly noticeable in Maris Otter which suffered the greatest loss of dry weight in the winter. From mid-December 1981 to mid-January 1982 the available PAR was almost zero, due to continuous snow cover.

Most winter barley varieties require a period of vernalisation before floral initiation can occur. Short days can substitute for cold vernalisation in some varieties (Jenkins, 1972; Jenkins & Whitehouse, 1972). All the varieties used in the present trial appear to have a low vernalisation requirement. Barling (1980b) observed that floral initiation in several barley varieties occurred within 30 days of sowing in mid-September in Southern England, with field temperatures of 8 to 9^{o}C. Hence, the vernalisation requirement is not great enough to maintain these cultivars in a vegetative condition through the winter, if sown in early autumn.

4.2 Seedling Emergence

This stage, though not delineated by any change at the stem apex, is important in marking the attainment of both autotrophy and exposure to the aerial environment. It seems likely that the base temperature for development from sowing to emergence was around 3°C for the two-row cultivars (Table 3.1.1). This agrees with Angus *et al.* (1981a) who found a base temperature of 2.6°C and a similar thermal time to emergence (80°Cd) with several barley cultivars grown in a wide range of Australian environments. However, there was no physiological reason for using this higher base temperature, and in the present experiments the pattern could have been confounded by the difference in sowing depth between S821 and S822. The mean seed depth in S821 was 34 mm and in S822, 44 mm. It is not known why the temperature response of the six-row cultivars should be slower than that of the two-row cultivars before seedling emergence (Table 3.1.1).

4.3 Floral Initiation

The first visible sign of floral initiation in the gramineae is seen at the stem apex as a sudden increase in the rate of primordium production (Austin & Jones, 1975; Langer, 1979). This is followed by the morphological change to the double ridge stage in the most advanced primordia (Table 3.1.4a). The double ridge stage (DR) is seen when the cauline ridges above the initial foliar ridges increase in size faster than the leaf primordia themselves.

In the present study, floral initiation was not coincident with the initiation of the primordium destined to become the collar on the ear. Between 1 and 12 primordia which eventually developed floral structures were present before floral initiation: there was no visible distinction between leaf and spikelet primordia at this stage. Barling (1980b) found a similar pattern in his study of winter barley development.

In plants grown at higher temperatures (eg spring sown or controlled environment) there is often a close association between collar initiation and the change in rate of primordium production at floral initiation. This has led to a lack of distinction, between the two events, in some of the literature (eg Appleyard, Kirby & Fellows, 1982; Gallagher, 1979a).

In a general, sowing later in the autumn prompted floral initiation in less thermal time, but at longer day lengths, than earlier sowings. It is known, that the floral initiation response is promoted by long days in many cultivars (Yasuda, 1982; Mansuri, 1969; Aspinall, 1966; Aspinall, 1969). However, there was little difference between treatments, in the mean photoperiod from emergence to floral initiation; the treatment which had the shortest time to floral initiation also had the lowest mean photoperiod during this phase.

It is difficult to equate these results with those found by other workers in controlled environments. In S81, floral initiation occurred at day lengths of about seven hours, which is well below the critical day length required for floral initiation in some varieties (Tingle, Faris & Ormrod, 1970; Aspinall, 1969). However, plants in this sowing had experienced longer day lengths soon after emergence. Both Igri and Gerbel showed a marked response in shortening the thermal time to floral initiation with later sowing (Table 3.1.4a). Maris Otter actually increased the thermal time to floral initiation with later sowing, though this was associated with dry weight loss, and low water soluble carbohydrate content (Section 3.2.3). It is possible that floral initiation is more dependant on an adequate carbohydrate reserve in the plant than on accumulated temperature or photoperiod *per se*. The actual mechanisms which control floral initiation in winter barley are still not known. Consequently, there is at present no unequivocal method for predicting the timing of this event in winter barley across a range of environments and cultivars. Different varieties exhibit different responses to confounded environmental controls.

The lower plant population in S81 than S82 may have caused slightly slower development in S81. Differences in plant population of this magnitude (200-400 plants m^{-2}) can cause a 1 to 3 day difference in development in spring barley, possibly because the plants' photoperiodic response is affected by the spectral composition of light, which changes with depth in a canopy (Kirby & Faris, 1970; Monteith, 1975; Holmes & McCartney, 1975).

4.4 Leaf Number

The final number of leaves did not differ greatly between treatments, however, the number was reduced on those varieties which had the shortest thermal time to the double ridge stage.

The foliar development of a primordium is assured as soon as vascularisation occurs. Vascularisation (in wheat) appears to be dependant upon the primordium reaching a critical size (Nicholls & May, 1964; Hutley-Bull & Schwabe, 1981). Once this size is reached the differentiation of the foliar ridge imposes some constraint upon the cauline ridge so that it may only develop into a tiller bud. Following floral initiation, growth and differentiation of the cauline ridge proceeds faster than that of the foliar ridge. The cauline ridge then imposes a constraint upon the subtending foliar ridge. The collar node arises from the foliar ridge which is just approaching its critical size for dominance over the cauline ridge, when floral initiation occurs (Hutley-Bull & Schwabe, 1981). Hence, the final number of leaves and the position of the collar on the apex is decided at the double ridge stage. The controlling factors are the number and size of initiated primordia at this time. Since neither the pre-floral rate of spikelet initiation (Table 3.7.1a) (presumably similar to the rate of leaf initiation[1]) or the thermal duration of leaf initiation (Table 3.1.3b), increased with later sowing, the thermal time to the double ridge stage would have been the factor which decided the final number of leaves on the mainstem.

Other workers have shown that, for a given environment or variety, there is often a clear relationship between leaf number and the time to double ridge stage (Aspinall, 1966; Appleyard, Kirby & Fellows, 1982). Also, since this relationship is partly dependant upon the photoperiodic response of the cultivar, the length of the vegetative phase, and therefore the final number of leaves, is a useful guide to the overall pace of plant development (Kirby, 1969; Appleyard, Kirby & Fellows, 1982). The initiation of fewer leaves on successive tillers (3 less on T1 than mainstem in S81) is entirely due to their shorter vegetative phase (Fletcher & Dale, 1977).

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[1] The rate of leaf initiation could not be determined in the present trials.

4.5 Floral Development

After the double ridge stage was reached further floral development to the glume primordia stage was delayed in thermal time if floral initiation occurred before mid-February. A similar pattern was not observed in Sonja winter barley either by Barling (1980a) or Kirby and Appleyard (1981a). However, in Kirby and Appleyard's (1981a) study, Igri winter barley remained at the double ridge stage from mid-November to January. Even in controlled environment conditions which promote rapid development, at least one barley variety has shown a time lag between attainment of the DR stage and further development (Deitzer, Hayes & Jabben, 1979).

In the present experiments the long delay seen in some of the treatments, may have been caused either by lack of assimilate supply, or by short photoperiods (less than 10 hours until 22 February at 56°N). This delay effectively reduced the divergence in development across all treatments, from 107 days at the start of the double ridge stage to 48 days at the triple mound stage (TM).

For a given variety, the later the TM stage was attained in the spring, the shorter the thermal time from the TM stage to anthesis (Table 3.1.4c). This gave near synchrony for mainstem anthesis in all varieties (a range of 10 days). This could have been due to the effects of longer photoperiods enhancing development subsequent to floral initiation, an effect which is well documented (Aspinall, 1966; Cottrell, Dale & Jeffcoat, 1981; Aitken, 1966; Äyräväinen, 1976). However, the widest range of mean photoperiod between the TM stage and anthesis was only between 14.0 hours in S81 and 15.3 hours in S822. Varieties differ in their response to photoperiod during this phase (Aspinall, 1966). In some varieties the response is to the increased PAR available in long days (Thompson & Matthews, 1982).

The photoperiodic response, during floral development, of the varieties used in these trials is not known, and the apparent effects shown in Table 3.1.4c can in fact be largely removed by using a higher base temperature when calculating thermal time. The regression of the rate of development (reciprocal of time) between the TM stage and anthesis, against the mean daily temperature in

this period shows that the base temperature for development should be around 4°C (Fig. 4.5). The thermal duration from the TM stage to anthesis, was comparable in all sowings if 4°C was used as the base temperature (Table 4.5).

TABLE 4.5: Thermal time, triple mound to start of anthesis (°Cd, base = 4°C)

Variety	S81	S821	S822
Gerbel	-	320	285
Athene	346	307	292
M. Otter	320	300	301
Igri	-	307	292
Video	303	-	-

Angus *et al.* (1981b) proposed a base temperature of 5.1°C for development in this phase in spring wheat. However, it is almost impossible to separate out photoperiod and thermal time since they will be correlated, and trials in a wider range of sowing dates or latitudes may reveal strong photoperiodic responses which were not revealed here.

Spikelet primordium initiation ceased when the awn primordium stage was reached on the stem apex. This agrees with Kirby and Faris (1970) for field grown spring barley. Other workers have recorded an earlier cessation of primordium initiation, at the stamen primordia stage (Cottrell, Dale & Jeffcoat, 1981; Nicholls & May, 1964).

Stem internode elongation began at the stamen primordia stage. The first node on the mainstem (GS31) was detected above the soil surface some days later at the awn initial stage. The cessation of primordium initiation and stem internode elongation are accompanied by a massive increase in gibberelic acid activity in the inflorescence (Nicholls & May, 1964).

4.6 Rate of Leaf Appearance

There was a close linear relationship between leaf appearance and accumulated air temperature above 0°C, as found by other workers (Gallagher, 1976; Baker, Gallagher & Monteith, 1980; Kirby, Appleyard & Fellows, 1982; Ellis & Russell, 1984; Hay & Tunnicliffe-Wilson, 1982).

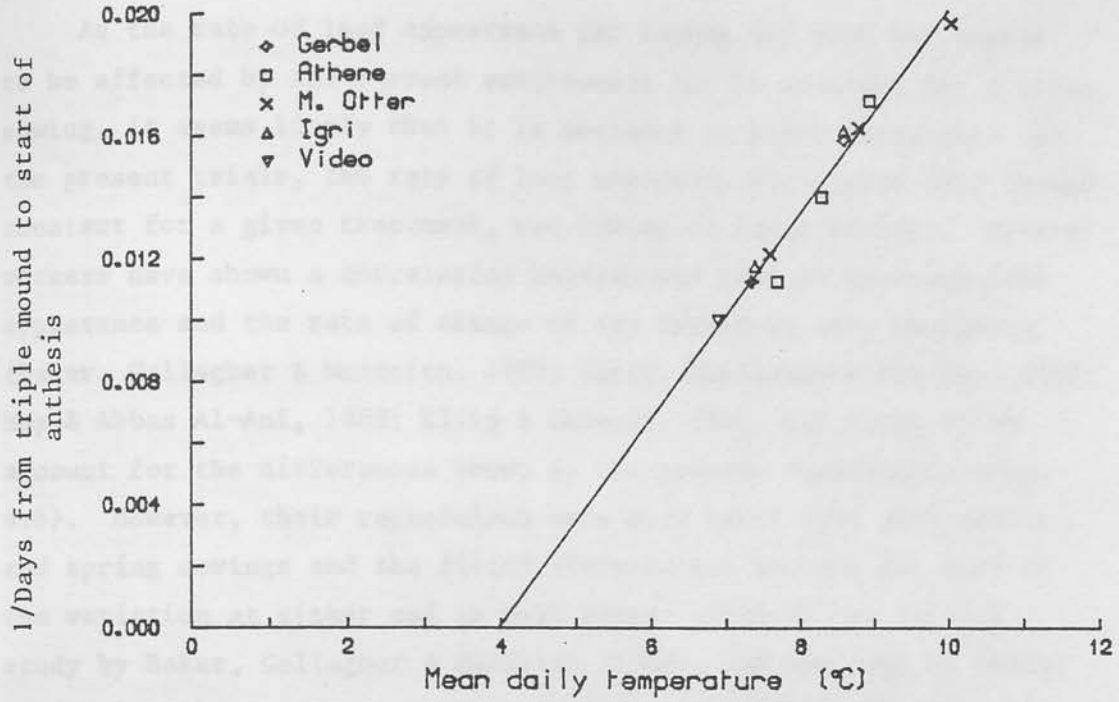

Fig. 4.5 The relation between the time from the triple mound stage to anthesis and mean daily temperature in that period.
Fitted line : $y = -0.013(\pm 0.0019) + 0.0034(\pm 0.00023)x$ accounted for 96% of the variance.

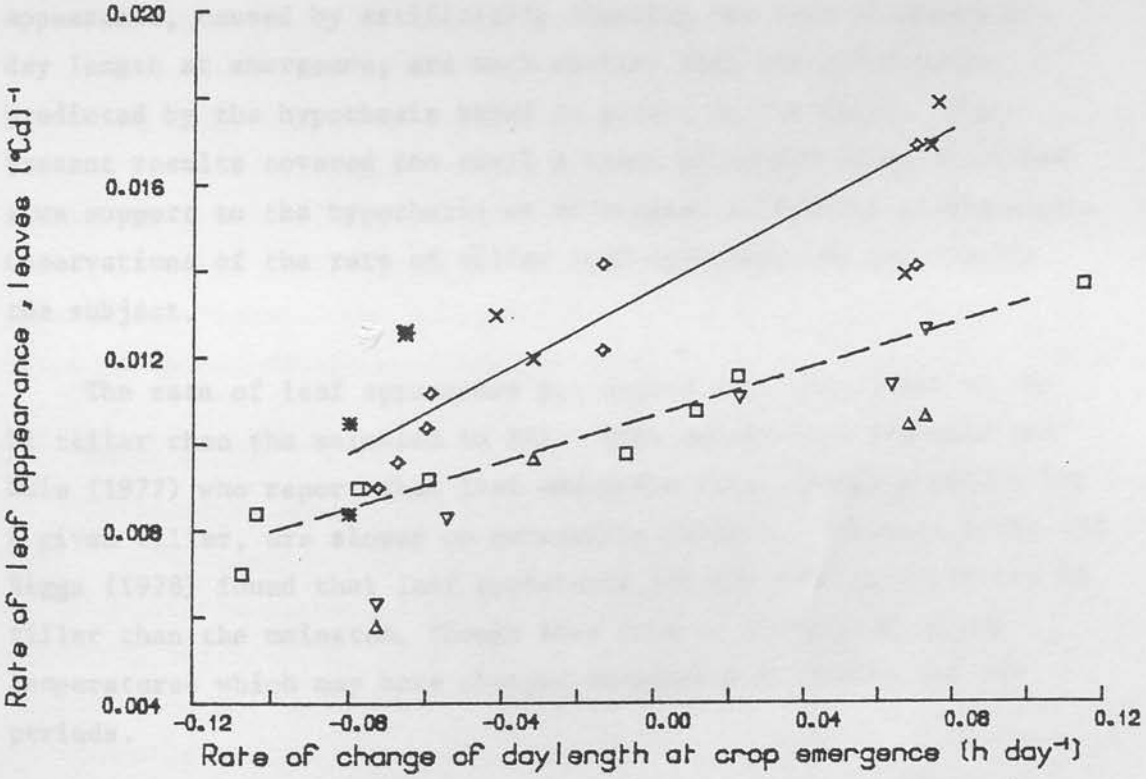

Fig. 4.6 The relation between the rate of change of daylength at seedling emergence and the rate of leaf appearance.
✱ this trial; × barley - Ellis & Russell, 1984; ◇ barley - Kirby, Appleyard & Fellows, 1982; □ wheat - Baker, Gallagher & Monteith, 1980; △ wheat, ▽ rye - Hay & Abbas al-Ani, 1983. The fitted lines are taken from Kirby, Appleyard & Fellows, 1982 and Baker, Gallagher & Monteith, 1980.

As the rate of leaf appearance per degree day does not appear to be affected by the current environment but is constant for a given sowing, it seems likely that it is mediated at plant emergence. In the present trials, the rate of leaf emergence per degree day, though constant for a given treatment, was faster in later sowings. Several workers have shown a correlation between the rate of mainstem leaf appearance and the rate of change of day length at crop emergence (Baker, Gallagher & Monteith, 1980; Kirby, Appleyard & Fellows, 1982; Hay & Abbas Al-Ani, 1983; Ellis & Russell, 1984) but these do not account for the differences shown in the present experiments (Fig. 4.6). However, their regressions have been based upon both autumn and spring sowings and the fitted lines do not account for much of the variation at either end in most cases. Only in the initial study by Baker, Gallagher & Monteith (1980), did the rate of change of day length at crop emergence provide a good fit to the rate of leaf appearance, over the complete range of sowing dates. Kirby and Appleyard (1983) have found that differences in the rate of leaf appearance, caused by artificially altering the rate of change of day length at emergence, are much smaller than the differences predicted by the hypothesis based on plants in the field. The present results covered too small a range of sowing dates to either give support to the hypothesis or to suggest a probable alternative. Observations of the rate of tiller leaf appearance do not clarify the subject.

The rate of leaf appearance per degree day, was slower on the T1 tiller than the mainstem in S81. This agrees with Fletcher and Dale (1977) who report that leaf emergence rates though constant for a given tiller, are slower on successive tillers. However, Kirby and Riggs (1978) found that leaf appearance *per day* was faster on the T1 tiller than the mainstem, though they give no indication of air temperatures which may have changed considerably between the two periods.

Fletcher and Dale (1977) suggest that the lower rate of tiller leaf unfolding as compared to the mainstem, is due to the lower growth potential and growth rate of the tiller which is established at inception. This is perhaps supported by the observation in spring barley, that at low plant populations there is little difference in the

rate of leaf emergence between the mainstem and tillers, but the difference increased with increasing population (Kirby & Faris, 1972). Kirby and Jones (1977) have also shown that the rate of mainstem leaf emergence can be increased by removing tillers, which questions the supposition that the rate of leaf emergence is decided at plant emergence.

4.7 Plant Morphology and Floral Development

The disparity found here between plant morphology and apical development stage (Section 3.1.5) has long been recognised as possible in temperate cereals (Andersen, 1955). This disparity is caused by the rate of leaf appearance and floral development being under different environmental control. However, the correlation between the two aspects is good for both spring barley and winter wheat (Andersen, 1955; Baker & Gallagher, 1983), which has enabled leaf counting to be a useful guide to plant development for these crops.

When investigating this relationship in spring barley Andersen (1955) found that the effects of changing plant density, fertiliser, moisture, light intensity and spring sowing date treatments, were small. However, he suggested that "if plants are grown under ..... winter culture ..... leaf counting will be insufficient to characterise their stage of development". This has been confirmed by the present experiments and questions the use of leaf counting as a guide to apical development stage in winter barley.

4.8 Conclusions

Temperature exerts the major influence on winter barley development. Vernalisation, photoperiod and available assimilate can also be effective in either stimulating or retarding development. Vernalisation requirements were readily met at field temperatures in the autumn. The photoperiodic effects, over the range of cultivars and environments tested, are hard to quantify as the actual plant responses are confounded by changes in temperature, available PAR, and ontogeny.

Floral initiation is not usually coincident with collar initiation in winter barley. The final number of leaves is dependant on the number and size of foliar primordia present at floral initiation. Leaf counting cannot be used as a guide to apical development in winter barley.

The practice of examining the primordial ear to assess the true development stage is preferable, especially when hormonal chemicals (hormone herbicides or growth manipulators) are to be applied to the crop.

There is an absence of phenological data on field grown winter barley in the literature; none have been presented with the necessary meteorological observations required to derive even simple models of development. Further work is required to determine the effects of temperature, photoperiod, vernalisation and available assimilate on development in different varieties of winter barley. In particular, the mechanisms which control floral initiation need to be investigated, to enable prediction of this event in different environments and cultivars. In order to predict the timing of mainstem elongation and anthesis, the control of floral development, including the possible delay in development between the double ridge stage and triple mound stage, needs to be examined.

CHAPTER V

WINTER HARDINESS

Over-wintering cereal plants are subject to a number of stresses which singly or in combination may be lethal. The environmental stresses causing winter injury are not necessarily related to low temperatures *per se* but to the sequence of temperatures, snow, ice, flooding and soil and crop conditions. The primary categories of winter injury are: soil heaving, smothering, physiological drought, and freezing of plant tissue.

The majority of plant loss during the severe winter of 1981-82 was caused by soil heaving. Direct frost kill and ice encasement also caused some plant loss. Freezing of plant tissue caused considerable leaf scorch, particularly in S821.

5.1 Soil Heaving

Soil heaving caused considerable plant death in S822. Frost heave has been considered the major cause of plant loss in other trials of late sown winter barley in this area (Russell *et al.*, 1982). The actual timing of plant death due to frost heave could not be established, because low temperatures delayed leaf senescence.

Damage to individual plants in S822 usually took the form of a clean break in the primary shoot below ground level, rather than breakage of the roots below the crown. A similar effect has been noted in autumn sown spring barley by Cox and Mason (1955). The break is caused by the lifting action of the top soil when frozen. The tensile strength of the mainstem (which is largely a function of size) could therefore be an important characteristic related to plant survival in these conditions. The late establishment of the S822 sowing meant that S822 plants were only at the one to two leaf stage with poor root development before winter. Maris Otter had the smallest plants in the autumn (best described as 'spindly') in both S82 sowings, possibly because of its small seed size, and this could account for the greater degree of plant loss due to soil heave in this cultivar. Small plants also give poor ground cover which increases the severity of soil freezing.

Soil heaving is particularly damaging when freezing and thawing are accompanied by high levels of soil moisture below the frozen surface zone (Kinbacher & Laude, 1955). This would have been the situation in late January after the snow thawed.

5.2 Freezing of Plant Tissue

Low temperatures can freeze plant tissue and if the apical meristem is frozen, plant death follows. The susceptibility of plant tissue to low temperature is dependant on the degree of hardening, tissue age, and physical protection from the environment.

Plant disease predisposes tissue to freezing injury (Smith & Olein, 1981). This may have been an important factor in the greater plant and leaf loss in the variety Maris Otter which always had higher levels of mildew (*Erysiphe graminis*) and rynchosporium (*Ryhnchosporium secalis*) than other varieties in the autumn. Even a slight infection with mildew can disrupt the hardening process (Koch, 1978; Frimmel, 1977; Grafius, 1981). Leaf scorch in S821 was greatest in older leaves as noted elsewhere for winter wheat (Marcellos, 1977) possibly due to poorer hardening ability, associated with the decline in photosynthetic capacity with leaf ageing (Dantuma, 1973). Leaves can only tolerate the extra-cellular freezing which occurs at low temperature, without membrane damage, if hardened (Single & Marcellos, 1981; Olein & Smith, 1981).

Survival of primordial ears depends on supercooling without freezing, this is helped by the blockage of ice growth by stem nodes (Single & Marcellos, 1981). Only in November 1981 were some small plants and coleoptile tillers in S821 killed directly by apical freezing. It is probable that the actual stage of apical development is of less importance in determining frost hardiness, than the insulation afforded to the apex by a compact crown below the soil surface prior to stem elongation (Shevtsov & Serkin, 1980; Jenkins, 1972). Vernalisation does not appear to be an effective means of keeping these winter barley cultivars in the vegetative state through winter (Section 4.3). However, in all sowings the apex remained below the soil surface until the start of stem elongation in April. The higher ratio of crown to total dry weight maintained by Athene through the winter could possibly have contributed to its better plant survival by insulating the apical meristem.

In S82 some plants were encased in ice for over 10 days in January. Ice encasement causes a combination of freezing and smothering, and can kill plants at temperatures not far below 0°C (Andrews, 1977; Andrews & Pomeroy, 1981; Smith & Olein, 1981). Maris Otter suffered total plant death in these areas while Athene suffered less; this was probably due to the lack of sufficient carbohydrate reserves in the smaller Maris Otter plants.

5.3 Plant Hardening

The effects of plant hardening could be seen in the unpredictable stress response of the plants during periods of frost (Section 3.2.2.). The relationship between the water soluble carbohydrate content in the spring and plant tissue death (Section 3.2.3), was probably related to the process of hardening. The increase in sugars in cold-hardening plants is accompanied by higher osmotic concentrations of sap and a reduction in tissue-water content (Trunova, 1982; Fejer, Hammill & Fedak, 1975; Huner, Palta & Carter, 1981). A high tissue-water content predisposes the plant to frost injury (Andrews & Pomeroy, 1981; Gusta, Fowler & Tyler, 1982). In January S82 the plants were briefly flooded due to snow-melt which could have led to an increase in tissue-water content.

5.4 Conclusions

In all sowings, plant development was such that apical meristems were protected by soil cover throughout the winter, and there was little direct plant death due to frost. Earlier sowing, or higher autumn temperatures, would not necessarily confer this protection, as the varieties used have a low vernalisation requirement.

Frost heave caused considerable plant death, particularly in the S822 sowing, due to the small size of plants. Plant loss due to ice encasement occurred in localised areas in both S821 and S822. In S822 Maris Otter, almost 40 per cent of the initial plant population was lost to leave 280 plants per square metre in the spring. Though this was still an acceptable mean plant population it disguises the fact that losses due to frost heave and ice encasement were usually in localised areas. In Maris Otter, these areas were too large for complete compensation by adjacent surviving plants, and so must have reduced potential yield considerably. This loss would have been much

greater if the crops had not been protected by snow cover during the coldest weather (Andrews, 1977), or if temperatures had dropped suddenly without a low positive temperature hardening period.

The loss of leaf area from S82 crops reduced crop growth rate in the spring, thus removing some of the advantage of winter over spring sowing. The actual loss of potential yield due to this delay could not be assessed.

The development of Maris Otter was delayed in the spring, in both S821 and S822. This was probably due to its low level of carbohydrate reserves after the winter compared to other varieties (Fig. 3.2.3a). Obviously, even in those Maris Otter plants which survived, almost all sugar reserves had been exhausted in overcoming freezing stress and disease, leaving little for rapid spring regrowth. There is a requirement for winter-hardy barley varieties, which can not only attain cold hardiness of leaf tissue, but also partition more assimilate to the crown before the winter, as in Athene. Such partitioning improves the plant's ability to withstand frost heaving, protects the apex from frost and provides carbohydrate storage for survival in ice encasement.

CHAPTER VI

DRY MATTER PRODUCTION AND PARTITIONING

6.1 Dry Matter Production

The traditional gauge of the efficiency of carbon fixation in a crop has been the measurement of the unit leaf rate (Watson, 1952). This method has limited usefulness for comparative work, due to the seasonal changes in solar radiation. In the present experiments, the changes in the unit leaf rate through the season followed the variations in absorbed PAR per unit green area, except during the autumn period when shoot growth was dependant on seed reserves rather than current photosynthate.

Trials of several winter barley varieties in two very different seasons at Cambridge, England, showed a positive correlation between plant dry weight in January, and seed size (Sage & Roffey, 1981; Sage & Roffey, 1982). So presumably it was the small size of Maris Otter seeds, which limited its plant growth rate in the autumn and winter. The effect on total crop dry weight is noticeable in both S82 sowings, when the seed rate was adjusted to give a standard number of plants per unit area.

Crop growth rate and total crop dry matter production were closely related to the amount of PAR absorbed over much of the season (Section 3.5). The relationship between crop growth and absorbed PAR has been demonstrated by other workers (Gallagher & Biscoe, 1978; Hawkins, 1982). The lower levels of dry matter produced per unit of PAR absorbed in S82 as compared with S81 are perhaps related to the lower nitrogen input in S82. However, the higher tiller loss in S82 than in S81 may have had a greater influence on the total crop growth rate (measured 'net' of turnover) than any restriction in nutrient supply. For example, Athene lost 600, 1800 and 900 tillers per square metre in S81, S821 and S822 respectively (Section 3.6.1). The high levels of tiller death in S82 may have been the cause of the lower conversion efficiency in these sowings, than the 3.0 g MJ^{-1} found by Gallagher and Biscoe (1978) for several crops of spring barley and winter wheat.

The ratio of CGR to PAR absorbed during winter did not appear to respond to temperature over periods of 10 days. This may have been due to the effects of leaf senescence on CGR during winter, or it may be that the CGR is reduced as the plant 'hardens' and CGR does not increase until temperatures rise for a prolonged period. However, short-term fluctuations in CGR due to temperature changes could have been hidden in the analysis since CGR was calculated from fitted curves. Mean temperatures between 1 March and 1 June (mean 10 day temperature range 3-16^{o}C) did not appear to influence the relationship between CGR and absorbed PAR, nor was there any consistent rise in the conversion efficiency over this period. Hence, it would appear that if Monteith's (1981) and Takeda's (1982) models of the negative response of photosynthesis to low temperatures are correct, the effects of this reduction are not carried through to crop growth rate. The proportion of assimilated carbon which is respired, increases with temperature in barley (Farrar, 1980). This increase is exponential in several species (Murata & Iyama, 1963). The respiration rate in winter barley is related to the night-time temperature, rather than previous photosynthetic gain (Fukai, Koh & Kamura, 1976). Hence, there should be a lower proportion of photosynthate lost through respiration at low winter temperatures which means that any reduction in crop growth rate due to low temperatures is less than the reduction in photosynthesis, which may partly account for the poor relationship between low temperatures and changes in the CGR.

The amount of dry matter produced per unit of PAR absorbed over the whole season, was similar to that in the period from 1 March to 1 June (Table 3.5.1). The high levels of plant loss during winter in S822 had little effect on the final ratio of dry matter production to absorbed PAR since these plants had absorbed very little PAR before their death. Similarly the reduction in the CGR to PAR absorbed ratio throughout winter would have had little effect on the final ratio, since the absolute values of absorbed PAR and CGR during winter were very low. Differences in the ratio of CGR to PAR absorbed after anthesis would greatly influence the final ratio, but measurement of absorbed PAR is difficult after anthesis because of the inclusion of the ear in the photosynthetic area, and effects of tissue ageing on the rate of photosynthesis (Biscoe, Scott & Monteith, 1975b; Takeda,

1979; Hawkins, 1982; Duntuma, 1973). However, in the immediate post-anthesis period in S82 the ratio of CGR to PAR absorbed actually increased as a marked reduction in available PAR did not appear to reduce the crop growth rate.

6.2 Canopy Development

The amount of PAR absorbed is dependant on the pattern of canopy development and its coincidence with seasonal changes in solar radiation. Canopy development prior to the start of stem elongation, is dependant on leaf appearance, expansion and senescence. In the present experiments, no single curve could be fitted to the LAI against thermal time before stem elongation.

Temperature is the main determinant of canopy expansion, since it controls both leaf emergence and expansion. Leaf appearance responds linearly to temperature, except during periods of severe cold. However, the response of leaf appearance to temperature is affected by the time of crop emergence, so different sowings can be expected to have different patterns of canopy growth (Section 4.6). Leaf extension in winter wheat and presumably winter barley, responds linearly to field temperatures between 5 and 20°C (Gallagher, Biscoe & Wallace, 1979; Kemp & Blacklow, 1982). However, at temperatures commonly experienced in the present trials, 0 to 5°C, the response is non-linear (Kemp & Blacklow, 1982; Gallagher, Biscoe & Wallace, 1979 (*Fig.3*)), thus one of the assumptions required for the calculation of thermal time is broken.

The use of thermal time to describe leaf growth in the graminae, is further complicated in the winter, since leaf growth responds to temperatures at the stem apex (Peacock, 1975). The apical temperature is closer to soil temperatures than to air temperatures at this time (Gallagher, 1976; Hay, 1978). Soil temperature in the 1981-82 winter remained below 0°C for long periods, even though air temperatures were above 0°C.

Winter kill and leaf senescence probably have a greater influence on the GAI than any of the problems associated with measuring the response of canopy expansion to temperature during the winter. In

both S82 sowings the LAI actually fell in the spring, due to high levels of leaf and plant loss.

The pattern of leaf emergence and senescence meant that there were never more than three live leaves on a mainstem before stem elongation. Hay and Tunnicliffe-Wilson (1982) noted that winter wheat crops had only three green leaves in this period. In the present trials, there were often only two leaves, and in the case of Maris Otter one leaf, alive at one time. Almost all Maris Otter leaves had a shorter life than equivalent leaves in other varieties, thus limiting its LAI. The leaf area per plant in Maris Otter in the autumn and winter was also restricted by the small seed size, since growth of the first two leaves is dependant on seed reserves (Milthorpe & Moorby, 1974). During the very cold weather in the winter of 1981-82 the thermal duration of leaves which unfolded in the autumn, actually increased. However, the lifetime of leaves which were extending during the winter, decreased. The reason for the shorter life of these leaves is not known, except to speculate that they were poorly adapted to photosynthesis in the higher temperature and irradiance levels in the spring, since the photosynthetic ability of leaves is affected by the irradiance experienced during development.

For all sowings the LAI reached by the start of stem elongation was 1.0 ± 0.3. Green, Vaidyanathan and Hough (1983) found that canopy growth in several crops of winter wheat could be best described by two straight lines against potential evaporation, intersecting at an LAI of 1.25 ± 0.01, which they suggested could coincide with the start of stem elongation. After stem elongation started in the spring, the LAI was supplemented by leaf sheath extension, though tiller initiation ceased and tiller death commenced. New leaves now unfolded faster than lower leaves died, to give a maximum of five live leaves per mainstem at ear emergence. For each sowing, this period of canopy growth (including: leaf, leaf sheath, culm and ear area) could be best described as a linear response to temperature. This might not have been the case if moisture or nutrients had been limiting.

The greater maximum GAI of S81 than S82 was almost entirely due to a higher number of tillers per unit area, the mean effect of which was to increase the total stem and ear area. Athene had a larger ear area than other varieties, due mainly to its greater awn area. Awns resemble the leaf blade in histological structure and are favourably placed for radiation interception (Hozyo & Kobayashi, 1969; Grundbacher, 1963). The main difference in canopy development between the two S82 sowings appeared to be that maximum GAI was reached later in crop development in S822 than S821, so that despite its low GAI during winter and spring, it had larger leaves with longer leaf longevity around the time of ear emergence, than the S821 crop. The pattern of canopy growth in S822 is more appropriate for interception of solar radiation in the summer and for partitioning assimilate directly to the grain. Thus the higher final yield of S822 than S821, despite later sowing and a shorter duration of growth, was probably achieved because its development pattern was better suited to the prevailing environmental conditions. S822 was able to maintain a higher growth rate than S821 during stem elongation and grain filling, whilst the higher autumn growth rates of S821 did not appear to contribute to grain yield.

6.3 Partitioning of Dry Matter

The efficient crop in terms of grain yield, partitions assimilate at each stage of growth towards the organ which will have the greatest effect upon one of the components of grain yield. Until a canopy is formed, this often means partitioning to leaf production in order to increase the interception of PAR. However, in winter cereals, leaf production in the autumn is often lost before spring; hence, autumn assimilate may be better used as storage reserves to enhance winter survival, or to increase early tiller production in order to give a long duration of growth for each surviving ear.

There were no consistent differences between the six-row and two-row types in partitioning of dry matter to the photosynthetic area. This is confirmed in a comparison of the two types by Äyräväinen and Paatela (1974). However, there were varietal peculiarities. Athene partitioned less of its initial seed reserves into leaf and root production than other cultivars, concentrating instead on growth of the 'crown' which may aid winter survival.

The main difference, in dry matter paritioning, between the two types, appeared later in the season; six-row varieties partitioned a greater proportion of total dry matter to the ear (Fig. 3.4.4b). This gave the six-row types a higher harvest index and a higher grain yield (Table 3.9.1). These differences, which were established by anthesis, were particularly evident in the S81 and S822 sowings. These sowings had more ears per plant then the S821 sowing, which emphasised the different crop structure of the six-row and two-row types. A similar pattern of preferential partitioning of dry matter to the ear prior to anthesis, leading to higher harvest index and high grain yields, has been described for several varieties of winter wheat (Brooking & Kirby, 1981; Bingham, 1976). This association between the partitioning of assimilate during ear growth and final grain yield, emphasises the importance of dry matter production and partitioning throughout growth.

The changes in specific leaf area through the season (Fig. 3.3.5) and its relationship with crop development, suggests that the leaf tissue acts as a storage reservoir for assimilate when demand from other sinks is low. Hence, leaf thickness increased (SLA decreased) before GS30, then fell rapidly throughout stem elongation as stored assimilate was used up, then increased again between the attainment of maximum stem length and the start of rapid grain filling. The cultivar Gerbel appeared more flexible in this respect, with greater leaf storage reserves used up in periods of high demand, particularly around the start of stem elongation.

Grain yield was better correlated with the amount of PAR absorbed after anthesis, than with absorbed PAR in any other period (Section 3.5.1). However, this could not have been a causal relationship since individual grain weight (which is the only component determined after anthesis) was the least variable component of yield. The majority of authors who have shown grain yield to be correlated with leaf area duration after anthesis have taken no account of changes in yield components (Welbank, French & Witts, 1966; Yap & Harvey, 1972; Spiertz, 1977). Only where a change in grain weight is the major cause of yield variation could it be suggested that the relationship is causal.

In the present trials a large proportion of the GAI after anthesis consisted of stem and ear area. The ear area inevitably increases with higher grain numbers per unit area, and the stem area increases with higher ear numbers per unit area. The size of the last three leaves on the mainstem is also positively correlated with floret survival (Section 7.2.2). Hence, a large GAI after anthesis is concomitant with a high number of grains per unit area (provided no severe moisture stress or disease intervenes).

The specific contribution of different organs to grain filling in the present trials, can only be assumed to have followed the pattern of green area senescence. The contribution made to grain filling by pre-anthesis assimilate, as noted particularly in S82, is now well documented (Biscoe *et al.*, 1975c; Daniels, Alcock & Scarisbrick, 1982). Austin *et al.* (1980b) calculated that a minimum of 10 per cent of grain yield must come from pre-anthesis assimilate since most of the protein in the wheat grain is present in the vegetative organs at anthesis (Austin *et al.*, 1978). In the present trials only the loss in stem weight rather than straw weight was calculated (Fig. 3.4.5). This loss was 450 gm^{-2} in S821 and 400 gm^{-2} in S822 with little measured loss in S81. The rise in specific leaf area during grain filling (Fig. 3.3.5), particularly in S821, coupled with the loss in leaf dry weight shows that leaf reserves were also used up. The inclusion of this loss in leaf dry weight did not significantly affect the analysis. Austin *et al.* (1980b)calculated from C^{14} studies, that only 73 per cent of the loss in dry matter from the straw between its maximum weight and maturity, is relocated to the grain, the rest being used for respiration. On this basis, the contribution of pre-anthesis stem reserves to grain dry matter was 55 per cent in S821 and 45 per cent in S822. Other studies have calculated the contribution of pre-anthesis reserves to grain weight in barley, as ranging from almost zero to a 100 per cent (Austin *et al.*, 1980b; Biscoe *et al.*, 1975c; Scott & Dennis-Jones, 1976; Yoshida, 1972; Daniels, Alcock & Scarisbrick, 1982; Hozyo & Kobayashi, 1969; Austin *et al.*, 1977). As found in the present study, the variation in the contribution of stem reserves is much greater between sowings than between cultivars, though six-row cultivars are possibly more dependant on stored carbohydrate than two-row cultivars (Austin *et al.*,

1978; Austin *et al.*, 1980b; Austin *et al.*, 1977). The overall picture is of a reserve of stored carbohydrate in the vegetative organs which varies in amount according to the balance between current photosynthesis and grain demand. When grain demand exceeds current photosynthesis, stored carbohydrates are mobilised to the grain. When current photosynthesis exceeds grain demand the pool of stored carbohydrate in the straw increases (Austin & Edrich, 1975). Even the products of current photosynthesis are stored temporarily, before actually entering the grain (Stoy, 1980). Therefore, straw weight can (i) increase between anthesis and maturity (Daniels, Alcock & Scarisbrick, 1982), (ii) first increase and then decrease (Austin *et al.*, 1980b; Warrington, Dunstone & Green, 1977), or (iii) first decrease and then increase (Rawson & Evans, 1971). Hence, the relative contribution of pre-anthesis assimilate, is dependant on demand for carbohydrate from the grain and the availability of current photosynthate to meet this demand. Several studies have concluded that the rate of grain filling is in some way predetermined and that this rate will be realised if source capacity (including storage reserves) is sufficient. Sink capacity will therefore govern grain yield until all storage reserves are exhausted, when current photosynthesis may exercise total control. It is quite possible therefore, that both sink control and source control can limit grain yield at different stages of this period. However, a large sink capacity is usually accompanied by a large GAI which presents a potentially large source capacity, both for PAR interception and storage of excess carbohydrates from current photosynthesis.

In the present trials, partitioning of dry matter to the grain after anthesis appeared to be largely controlled by sink demand, since (i) both the duration of whole crop grain filling and absorbed PAR after anthesis were greatest in S81, yet its individual grain weight was not greater than in S82, (ii) grain filling in S82 continued at the expense of weight loss from the straw.

6.4 Conclusions

Crop growth rate was closely related to the amount of PAR absorbed over much of the season. The relationship did not hold

during initial growth (due to the contribution of seed reserves), after anthesis (due to tissue ageing) and during winter (due to low crop growth rates related either to hardening or net loss of leaf). Low temperatures did not appear to directly alter the relationship between absorbed PAR and CGR, though the method used in the present experiments of calculating these values from fitted curves, may have hidden any short-term response to temperature. Further work is required to determine the relationship between absorbed PAR and crop growth, when carbon accumulation may be limited by low temperature, plant hardening, or moisture and nutrient deficiency.

There was a suggestion that the six-row types utilised solar radiation more efficiently. The highest yielding treatments had the best conversion figures. The six-row types also partitioned more of their dry matter to the ear than the two-row types.

The development pattern of S822 was better suited to the prevailing environment than that of S821. S822 was able to maintain a high growth rate during stem elongation and grain filling, whilst the higher autumn growth rate of S821 did not appear to contribute to grain yield. These differences were perhaps related to differences in canopy development. The maximum GAI was reached later in crop development in S822 than in S821. The pattern of canopy growth in S822 was more appropriate for interception of solar radiation and partitioning assimilate directly to the grain. The higher maximum GAI in S81 than S82 was almost entirely due to its greater ear population, which greatly increased both stem and ear green area. The correlation between the PAR absorbed after anthesis and grain yield was largely due to a correlation between the GAI at anthesis and the number of grains per unit area.

Canopy development before GS31 could not be modelled. Many factors make this difficult for an over-wintering crop, not least of which are leaf senescence and plant death. For all sowings, the GAI reached by the start of stem elongation was 1.0 ± 0.3. From this time until its maximum value, GAI increased linearly in thermal time, though this might not have been the case if moisture or nutrients had been limiting. Hence, if the timing of stem elongation could be predicted, the pattern of GAI development could be modelled. Defining

an accurate GAI before stem elongation is less important since both insolation and light interception are low. However, the pattern of canopy development in the present experiments requires confirmation from trials in a wider range of environments in which GAI is recorded in conjunction with crop development.

The vegetative organs store carbohydrate in varying amounts according to the balance between current photosynthesis and sink demand. The changes in specific leaf area with ontogeny reflected this storage capacity. Partitioning of dry matter to the grain after anthesis appeared to be controlled by sink demand. Further work is required to identify the factors involved in sink demand, not just in the grain filling period, but throughout growth. The factors controlling the supply of carbohydrate to those tillers and spikelet primordia which survive to anthesis may be of greater importance than those which control assimilate supply to the grain. However, the arguments over sink and source control of grain weight and over the relative contributions of different sources of carbon are futile until it is shown that one source provides assimilate to the grain more efficiently than another. The observations by Daniels, Alcock and Scarisbrick (1982) that high grain yields in barley are associated with large positive increases in straw weight after anthesis, suggests that the use of stored reserves for grain filling limits grain size, possibly because it is not as efficient a source of carbon as current photosynthate.

CHAPTER VII

COMPONENTS OF YIELD

The grain yield of barley is comprised of three components: individual grain weight; the number of grains per ear; and the number of ears per unit area. The latter two are the most variable for a given spring barley variety over a wide range of environments (Gallagher, Biscoe & Scott, 1975; Dyson, 1977). The number of grains per unit area is therefore seen as the most important component of spring barley yield. In the present experiments, the number of grains per unit area was the basis for the higher yield in S81, and for almost all grain yield variation between treatment replicates.

Gallagher, Biscoe and Scott (1975) emphasised the overriding control of grain yield by grain number in spring barley. However, their analysis also shows that variation in grain weight at a given grain number can cause differences in grain yield of up to 1.5 tonnes per hectare. Hence, differences in 1000 grain weight cannot be dismissed. Higher grain weight was the main reason for higher yields in S822 than S821.

For the six-row varieties, the number of grains per ear was the most important component of grain number per unit area, both between and within treatments. For the two-row cultivars, the number of ears per unit area was of overriding importance. This appears to be a consistent difference between the two-row and six-row types (Äyräväinen, 1976).

The formation of each of these components will now be considered in detail.

7.1 Number of Ears per Unit Area

In the present trials, the S81 sowing compensated for its low plant population by retaining many more tillers to maturity. The importance of tillering ability in the cereal plant to compensate for low plant populations, has long been recognised (Engledow & Wadham, 1923; Engledow, 1926). There is competition between tillers and the main shoot, even during initiation and early growth (Kirby & Jones, 1977), and it has been suggested that a high population of

uniculm plants should out-yield a lower population of multiculm plants with the same final ear population (Donald, 1968). However, Borojević and Kraljević-Balalić (1980) have shown that intra-plant competition in winter wheat plants with 2 to 3 tillers, may not be as great as inter-plant competition between uniculm plants maintained at the same stem density, because tillered plants are bigger with better rooting systems in the winter and do not start inter-plant competition until later. It can also be argued that because a population of tillers will have a wider range of development stages than a similar population of mainstems, it is more flexible in its response to the environment, as successive tillers pass through critical development stages at slightly different times. Similarly, the GAI curve of successive tillers will be staggered, giving a broader peak to total GAI at anthesis, as seen in S81. Extending the duration of maximum GAI is more efficient than raising the maximum since the proportion of PAR absorbed rises asymptotically towards an upper limit, with increase in GAI. Any reduction in yield due to unproductive tillers is deemed to be slight if moisture is not limiting, because their minerals are largely returned to the plant, and competitive stresses (in winter wheat at least) come mainly from productive shoots (Kirby & Faris, 1972; Jones & Kirby, 1977; Simpson, Lambers & Dalling, 1982; Bremner, 1969). Hence multiculm plants may be more desirable than uniculms even if the required ear population could be obtained with uniculms. For efficient harvesting however, it is important for the tiller grains to mature more rapidly so that all the grains reach maturity simultaneously.

7.1.1 Tiller production

No observations were made of tiller bud initiation, but in S81 Video tillers emerged in the axil of all the mainstem leaves up to the seventh. Kirby and Faris (1972) found no tiller buds at positions higher than T5 in spring barley, even at low plant populations. Hence, it appears that winter sown barley has more tiller sites available than spring sown barley as a consequence of its longer vegetative period.

The time of first tiller emergence (GS21) differed between sowings, but not consistently between genotypes. It was not

correlated with thermal time from sowing, calendar date or the number of mainstem leaves unfolded. The thermal time to GS21 and the number of leaves emerged at GS21 were both greatest in S822, which did not tiller until the spring. This sowing would have had a severe shortage of assimilate during the winter which would delay tiller growth and emergence.

The duration of tillering also varied between sowings, although only in S81 was there any difference btween the two-row and six-row types (Section 3.6.2). In S821, which had the highest tiller population, maximum tiller numbers were recorded a few days before GS31. For all varieties in S822 and for Athene in S81, the maximum was reached at GS31, but the two-row cultivars in S81 did not reach their maximum until 25 days after anthesis. The duration of tillering was longer in S81 than S82 for three reasons: shorter time to GS21 (due to early sowing and good weather); longer thermal time from GS21 to GS31 (due to earlier sowing and lower plant population); and continued tillering after GS31 (due to less inter-plant competition and higher nitrogen application (McLaren, 1981)). Similarly, the time to GS21 was shorter, and duration from GS21 to GS31 was greater, in S821 than S822 because of its earlier sowing.

Although there was no specific link between the time a leaf emerged and the time its subtending tiller emerged, successive tillers emerged later relative to leaf emergence, presumably due to increasing competition for light and nutrients. The faster rates of 'whole plant' tiller emergence per degree day in later sowings were related to faster rates of leaf emergence on the mainstem. The rate of 'whole plant' tiller emergence per mainstem leaf, did not differ consistently with date of sowing from about 1.1 tillers per leaf (though confidence limits were large); this supports the suggestion that the low plant population of S81 produced more tillers per plant than other sowings because of a longer duration of tillering, rather than an increased rate of tillering. The rate of tiller production per mainstem leaf shown here (Table 3.6.2c) is low compared with spring sown crops, where the ratio may be nearer to 2.0, but the duration of tillering much shorter (Kirby & Riggs, 1978; Gallagher, Biscoe & Scott, 1976).

The higher maximum tiller numbers of two-row cultivars than six-row cultivars were not statistically significant, but were consistent in all sowings which suggests that they may be true differences. In S81, the lower value for Athene could be attributed to its earlier cessation of tillering. In S821 and S822 however, the six-row varieties must have had a slightly lower tillering rate which was not shown up by the analysis. Kirby and Riggs (1978) when comparing the six-row Clermont with the two-row Proctor, found that the delay in tiller emergence at each mainstem site depended only on the tiller site, not the genotype. Clermont appeared to have fewer tillers per plant because of a shorter duration of tillering and faster development than Proctor.

Common and Klinck (1982), on the basis of experiments with several six-rowed spring barleys, suggest that a limited tillering synchronous genotype may not exist at present among six-rowed barleys. The present study shows only a slight difference in the tillering behaviour of the six- and two-row types, before mainstem elongation.

Tiller emergence after anthesis was evident only in the two-row cultivars, but these tillers did not contribute to grain yield, and may have slightly reduced the yield of productive shoots.

The composition of emerged tillers on S81 plants followed the expected order of initiation, except for the coleoptile tiller (TC), (Table 3.6.4). Variability in the emergence of TC is common (Cannell, 1969a; Cannell, 1969b; Kirby & Riggs, 1978; Gallagher, Biscoe & Scott, 1976; Fletcher & Dale, 1974). Rapid growth of initiated tiller buds is delayed by a reduced supply of assimilate and nutrients (Fletcher & Dale, 1974). Such a delay can cause tiller death before emergence (Kirby & Faris, 1972). The tiller bud is probably present in the dry grain (Fletcher & Dale, 1974) and so may die in the often adverse conditions between germination and seedling emergence.

7.1.2 Tiller survival

Final ear populations were neither related to initial plant populations nor to maximum tiller populations, but were related to

differences in tiller survival between sowings and genotypes.

The first tillers were seen to die soon after GS31 in all sowings (excluding winter losses), but senescence must have started several days before this time. A tiller stops producing leaves about seven days before the first leaves are seen to die (Kirby & Riggs, 1978) and may show internal signs of death (by different staining reactions) some 2 to 3 weeks before shoot death (Krishnamurthy, 1963). The youngest tillers normally die first (Kirby & Ellis, 1980). The probability of a tiller growing to maturity depends on its size (and so its autonomy) at the start of stem elongation on the parent shoot (Kirby & Riggs, 1978). No measurements were made of tiller size, but it is likely that S81 tillers were larger than comparable tillers in either S82 sowings because of their earlier emergence. The youngest tillers to survive in S81 Maris Otter would have been the T4 tillers which emerged at the end of January, two months before GS31 (thermal time 300°Cd). In S822 Maris Otter some T2 tillers which emerged at the end of March, one month before GS31 survived (thermal time 200°Cd). Hence, the higher ear populations in S81 were due primarily, to the longer duration of tiller growth before GS31 in this sowing. The differences in ear population between sowings were primarily between the two-row cultivars. The six-row cultivars exhibited apical dominance to a far greater degree after GS31. This difference between the types in tiller survival is normal (Kirby & Riggs, 1978) and is the main reason for their dissimilar ear populations. Poor tiller survival in six-row cultivars could not be explained by the size of tillers at GS31 since they emerged at the same time as comparable tillers in two-row types. It may be that the critical size for survival at GS31, is larger in the six-row types. However, there was some evidence in six-row varieties that even some culms about to reach ear emergence, died soon after mainstem ear anthesis.

7.2 Number of Grains per Ear

The final number of grains per ear is determined by: the rate (Rs) and duration (Ds) of initiation of spikelet primordia; the proportion of spikelet primordia surviving to form florets at anthesis (Sf); and the proportion of viable florets which are fertilised and set grain (Ff) [ie grains/ear = Rs x Ds x Sf x Ff]. It is difficult

to establish the environmental causes for differences in these components between sowings, as different barley varieties are known to differ considerably in their response to environmental control of grain number (Tingle, Faris & Ormrod, 1970).

The final grain number per ear, was more closely related to 'Sf' than to the maximum number of spikelets produced. Variation in 'Sf' has been reported elsewhere as the major cause of differences in grain number per ear between different sowings and varieties (Russell *et al.*, 1982; Tingle, Faris & Ormrod, 1970). However in other experiments, 'Sf' has been relatively stable and the maximum number of primordia produced, has been of greater importance (Ellis & Russell, 1984; Kirby & Appleyard, 1978).

7.2.1 Spikelet initiation

Primordia which eventually formed grains were initiated both before, and after floral initiation at meristem elongation (Section 4.3). The rate of primordium initiation per degree day increased after floral initiation. The later sowings produced fewer spikelet primordia than early sowings because the reduction in 'Ds' with later sowing was relatively greater than the increase in 'Rs' (Section 3.7.1).

The duration of initiation (Ds) was limited by the progress of development in the oldest spikelets. Primordium initiation stopped soon after the awn initial stage was reached. The thermal time from sowing to floral initiation, and from floral initiation to the awn initial stage, was shorter in later sowings (Section 3.1.4).

Although low levels of PAR have been shown to reduce spikelet numbers by decreasing 'Rs' to a greater degree than any increase in 'Ds' (Aspinall & Paleg, 1963; Friend, 1965; Rahman, Wilson & Aitken, 1977), levels of PAR in the field are normally higher than those used in these controlled environment experiments. In the present study, the treatments which had the lowest levels of mean daily PAR during spikelet initiation (S81) actually produced more spikelets than those with higher levels of PAR (S822).

Higher temperatures hasten cereal crop development more than they increase the rate of primordium initiation and so fewer spikelets are initiated (Rahman & Wilson, 1978; Friend, 1965). Long photoperiods also hasten ear development to a greater degree than they increase 'Rs', thus giving a lower maximum number of primordia (Kirby & Appleyard, 1978; Fairey, Hunt & Stoskopf, 1975; Aspinall & Paleg, 1963; Rahman & Wilson, 1977; Kirby & Ellis, 1980; Appleyard, Kirby & Fellows, 1982). Barley varieties differ greatly in their photoperiodic response for this aspect of development (Kirby & Appleyard, 1978; Tingle, Faris & Ormrod, 1970). The photoperiodic response of the varieties used here is not known.

It is probable that the faster rates of initiation per degree day, and shorter duration of initiation in later sowings, were caused by a combination of higher daily temperatures and longer photoperiods. It was not possible to distinguish between the separate effects of these two factors on spikelet production in the present experiment.

There was no consistent difference between six-row and two-row cultivars in the rates of rachis level initiation. However, slightly fewer rachis levels were initiated in the six-row types than in the two-row types (except Video). Tingle, Faris and Ormrod (1970) found that six-row cultivars generally produced fewer rachis levels than two-row cultivars in a study of several varieties, in a controlled environment.

7.2.2 Spikelet abortion

The death of primordia at the distal end of the ear prior to anthesis, coincided with a massive increase in stem length, plant dry weight, ear dry weight and awn length. This, and the fact that spikelet survival (Sf) was lowest, and tiller loss was highest in S821, suggests that competition for assimilate within the plant leads to spikelet abortion, as noted elsewhere (Gallagher, Biscoe & Scott, 1976; Kirby & Faris, 1970). This suggestion is supported by the results of work in which competition within the plant has been increased during ear growth.

Moisture stress at this time reduces the number of grains per ear (Aspinall, Nicholls & May, 1964). Tiller removal increases spikelet survival on the mainshoot (Kirby & Jones, 1977). Isogenic barley lines differing only in awn length have more florets per ear in awnless lines (Faris, 1974). A positive correlation, between available PAR and 'Sf', during the period of spikelet abortion, has been demonstrated for both barley and wheat (Evans, 1978; Willey & Holliday, 1971). However, although daily PAR in the period from tip death to anthesis was greater for S821 and S822 sowings (9.2 MJ m^{-2}) than for S81 (7.8 MJ m^{-2}), 'Sf' was not significantly higher.

The main light-intercepting organs on the mainstem in this period were leaf 2^t ($L2^t$) and leaf 3^t ($L3^t$) in all treatments (flag leaf = $L1^t$). $L3^t$ unfolded soon after the time of maximum primordia and continued to photosynthesise until well after ear emergence. $L2^t$ unfolded within five days of $L3^t$ and so contributed considerably to photosynthesis in the spikelet abortion period. The flag leaf ($L1^t$) unfolded near the end of the abortion period and therefore probably had little effect upon the number of florets present at anthesis. For three varieties which had a significantly larger leaf area (Leaf 2^t and Leaf 3^t) in S822 than S821, there was also a significant increase in 'Sf'. One variety had no significant change in either 'Sf' or leaf area (Fig. 7.2.2). This relationship was not improved by including mean daily PAR during the spikelet abortion period. Williams and Hayes (1979) found a good correlation between the dry weight of $L3^t$ and the final number of grains on the mainstem ear in both six-row and two-row cultivars. This relationship could hold either because $L3^t$ is the main photoreceptive organ during spikelet abortion, or because $L3^t$ is expanding during spikelet initiation, and any constraints upon its size may also reduce the maximum number of primordia produced.

From Kirby, Appleyard and Fellows (1982), it appears that later autumn sowings of Sonja winter barley produced larger leaves at $L3^t$ and $L2^t$. They suggested that leaves extending in the period from November to February inclusive, did not increase in size relative to the preceding leaf, so early sowings had smaller final leaves than late sowings. Gallagher (1976) found that the mean leaf extension rate per degree day increased with leaf position in the spring.

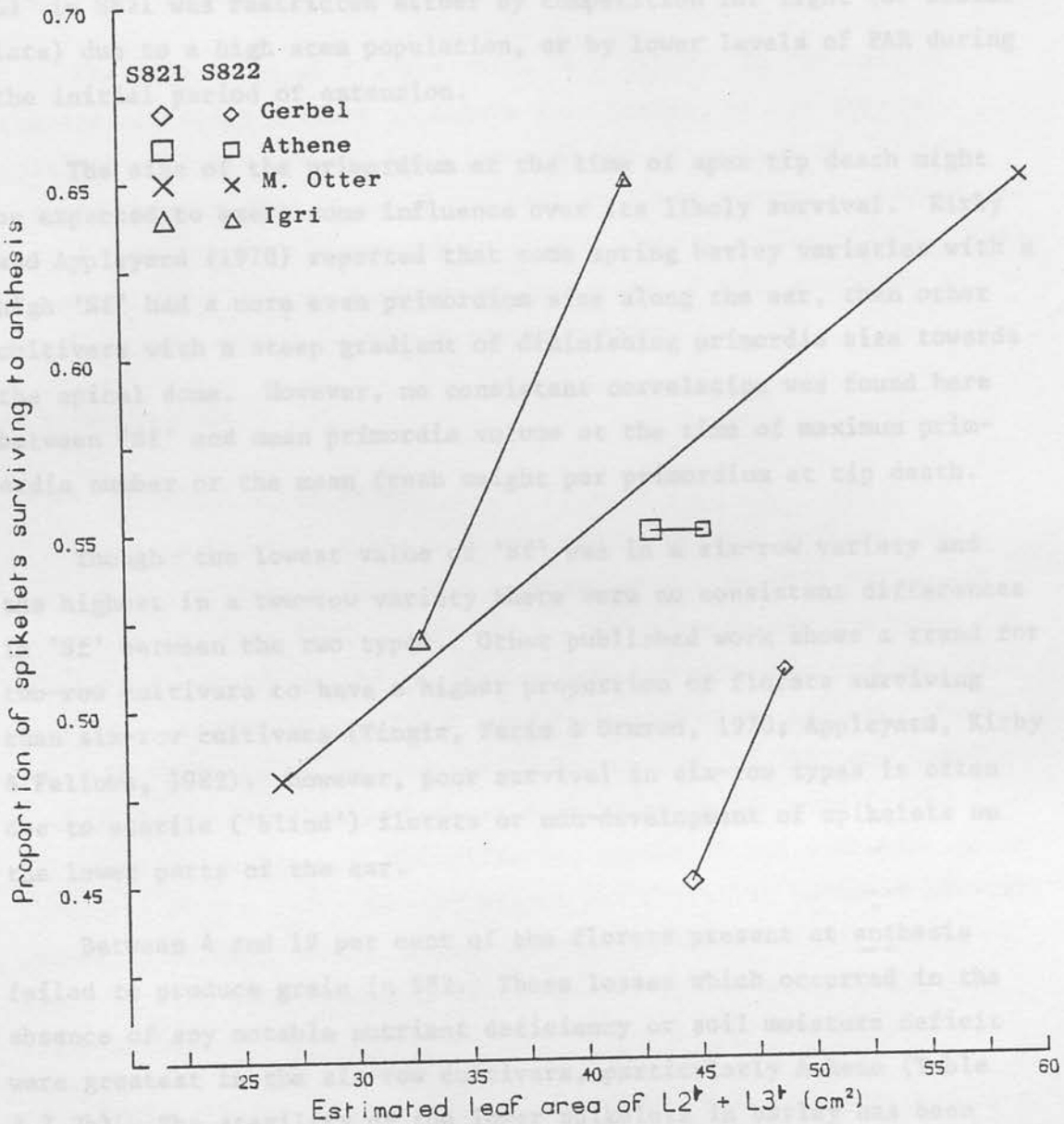

Fig. 7.7.2 The relation between the proportion of spikelets survivng to anthesis and the size of leaf 2^t + leaf 3^t. Leaf area taken as half the product of length x maximum width.

This may have been a response to longer days or to higher levels of available PAR. In the present study no records were made of leaf extension but leaves 2^t and 3^t in S822 unfolded within a few days of comparable leaves in S821. It is possible that the size of $L2^t$ and $L3^t$ in S821 was restricted either by competition for light (or assimilate) due to a high stem population, or by lower levels of PAR during the initial period of extension.

The size of the primordium at the time of apex tip death might be expected to exert some influence over its likely survival. Kirby and Appleyard (1978) reported that some spring barley varieties with a high 'Sf' had a more even primordium size along the ear, than other cultivars with a steep gradient of diminishing primordia size towards the apical dome. However, no consistent correlation was found here between 'Sf' and mean primordia volume at the time of maximum primordia number or the mean fresh weight per primordium at tip death.

Though the lowest value of 'Sf' was in a six-row variety and the highest in a two-row variety there were no consistent differences in 'Sf' between the two types. Other published work shows a trend for two-row cultivars to have a higher proportion of florets surviving than six-row cultivars (Tingle, Faris & Ormrod, 1970; Appleyard, Kirby & Fellows, 1982). However, poor survival in six-row types is often due to sterile ('blind') florets or non-development of spikelets on the lower parts of the ear.

Between 4 and 19 per cent of the florets present at anthesis failed to produce grain in S82. These losses which occurred in the absence of any notable nutrient deficiency or soil moisture deficit were greatest in the six-row cultivars, particularly Athene (Table 3.7.2b). The sterility of the lower spikelets in barley has been studied extensively by Kinebuchi (1962) who found that there were different varietal responses. He concluded that failure of these florets was due to insufficient assimilate supply to the ear after flag leaf emergence, and found a significant negative correlation between the size of green area above the flag leaf node and the number of lower spikelets that were sterile. The flag leaf of six-row cultivars supplies assimilates to many more florets than

that of the two-row types, yet in the present trials the area of the flag leaf was not proportionately larger in the six-row cultivars. Athene, which had more sterile lower florets than Gerbel also had a significantly smaller flag leaf than Gerbel in both S82 sowings (Table 3.3.3).

The proportion of florets which were 'blind' in the rest of the ear was again greater in Athene than Gerbel, or the two-row cultivars. Other workers have reported the percentage of 'blind' florets ranging from 14 to 28 per cent in three six-row cultivars and 5 to 8 per cent in six two-row cultivars (Sage & Roffey, 1983). They suggested that 'blind' florets may be caused by poor synchrony of the flowering events in winter barley cultivars.

7.3 Grain Size

7.3.1 Mainstem grain weight

Mean grain size on the mainstem varied between sowings, but only within a limited range for each variety. The S822 sowing had larger grains than S821. Most of the variation in maximum grain dry weight and ear dry weight per grain, both between and within cultivars, was evident in ear fresh weight per floret at anthesis (Fig. 3.8.2b). This is in agreement with Scott *et al.* (1983) who found a significant correlation between final grain weight and floret weight at anthesis, both for different varieties and different grain positions on the ear. Ear dry weight per floret at anthesis consists primarily of awn, rachis, lemma and palea. The final dry weight of awns, rachis, and presumably the lemma and palea, was reached soon after anthesis.

Grain filling in the present experiments was characterised by a linear phase of grain growth following a lag period of 10 to 14 days immediately after anthesis. Final grain weight is determined by both the rate of dry matter accumulation and the duration of the linear phase of growth. The rate of grain growth in the linear phase appears to be determined early in the grain filling period as it does not fluctuate with changes in available PAR (Evans, 1978).

Scott *et al.* (1983) demonstrated a clear relationship between initial caryopsis size and the rate of grain growth in barley. In

the present study, differences between treatments in mean grain growth rate were correlated with ear fresh weight per floret at anthesis, though the small number of harvests in this period make analysis difficult (Fig. 3.8.2d, Table 3.8.2c). Maris Otter was the exception to this pattern; its small grain size resulted from a shorter duration of grain growth rather than a slower rate of grain filling. The relationship between floret size and final grain weight in the present study, suggests that the potential grain size had been determined by the time of anthesis, and that this potential was not limited by the supply of assimilate to the grains after anthesis. This is further confirmed by the observation that the presence of sterile florets failed to influence the size of neighbouring grains (Fig. 3.8.3).

If there is a causal relationship between potential grain size and the size of florets at anthesis, as suggested above (either due to initial ovary size or the physical limitations imposed by the lemma and palea), it is important to determine which factors affected initial floret size and growth before anthesis.

The relationship between mean ear volume per potential grain at the triple mound stage and final grain weight (Fig. 3.8.2a) suggests that differences in initial primordium size, both between and within genotypes, may influence potential grain weight. Maris Otter did not fit into this general relationship so the reason for its small grain size must be found in subsequent primordium growth. It has been suggested that the typical variation in grain weight along a barley ear (Fig. 3.8.3) stems from differences in primordium size (Kirby, 1977). The size of successive primordia when initiated, increases from the collar until over half the primordia are initiated and then declines, while the RGR of individual primordia increases from the collar (Kirby, 1977; 1975). The effect of this pattern is to produce at the time of maximum primordia number, an embryo ear in which the heaviest and most advanced spikelets are found in the lower mid portion of the ear (Kirby, 1975; Nicholls & May, 1963).

In the present trial, differences in initial primordium size between sowings were probably related to assimilate supply. Crops in S822 absorbed more PAR during the period from collar initiation

to triple mound stage than did S821 crops. For example, in this period S821 Gerbel absorbed 13 MJ m^{-2} PAR and S822 Gerbel 45 MJ m^{-2} PAR, yet both had a similar number of stems m^{-2} at the triple mound stage. Hence, moving the spikelet initiation phase into a period with more available PAR may give larger spikelets, though it is possible that the smaller spikelets in S821 were due to lower mean daily temperatures and freezing stress during the ear initiation period. Ellis and Kirby (1980) suggested that, the differences they recorded in grain size between trial sites, were caused by low levels of PAR during spikelet initiation at one site, resulting in small spikelet primordia.

During the main period of ear growth, from the maximum primordia number to anthesis, ear growth is exponential (Kirby & Riggs, 1978; Scott *et al.*, 1983; Brooking & Kirby, 1981). The duration of this period was shorter for Maris Otter than other varieties, due to its later development, which could account for its smaller floret size at anthesis. With a relative growth rate of 0.02 $(^{o}Cd)^{-1}$, spikelet fresh weight would double in 50^{o}Cd (about 5 days). Variation in the duration of ear growth, resulting in different ear weights at anthesis has been noted elsewhere (Kirby & Riggs, 1978).

Gallagher (1979b) found that crop thinning during ear growth had no effect upon subsequent grain size. This suggests that spikelet growth may not be limited by photosynthetic capacity at this time but rather by assimilate demand from the spikelet itself, which would be a function of initial size. However, shading of the crop during ear growth can reduce grain weight in some circumstances (Willey & Holliday, 1971).

Whole crop 1000 grain weight followed the pattern of mainstem maximum grain weight. Whole crop mean grain weight was only a slightly lower percentage of mainstem grain weight in S81 than in S82, despite there being many more tillers per plant in S81. Assimilate supply did not appear to limit grain size in S81 since there was little loss in stem weight after anthesis (Fig. 3.4.5). In S82 the loss of dry matter from the stems after anthesis appears to have acted as a buffer to support normal grain growth, enabling grains to achieve their potential weight (Section 6.3).

7.3.2 Ear type

The mean grain weight of six-row cultivars is normally lower than that of two-row cultivars, though some six-row cultivars have high 1000 grain weights (Williams & Hayes, 1979). Maris Otter, used in the present trials, is a small grained variety with its grain size nearing the minimum expected in two-row genotypes. The six-row cultivars had heavier median grains than the two-row cultivars in the present study. However, the lateral grains on the six-row cultivars weighed only 70 to 75 per cent of the median grains, and contributed about 60 per cent to total grain weight on the ear.

Scott *et al.* (1983) found that husk dry weight was smaller for the lateral grains than for the median grains in one six-row variety and that husk dry weight was well correlated with final grain dry weight. They also found that the ratio of lateral to median carpel weight at anthesis, was similar to the lateral to median caryopsis weight ratio at maturity. The difference between lateral and median floret size at anthesis was matched by lower rates of grain growth, in the linear phase, for lateral grains (Scott *et al.*, 1983).

The percentage increase in lateral grain weight between S821 and S822 was greater than the percentage increase in the weight of median grains suggesting that the potential size of lateral grains is more variable than that of the median grains.

It is not known why the size of lateral grains on one side of the ear should follow a progression distinct from that on the other side (Fig. 3.8.3). One explanation may be that they would be served by different vascular bundles, if the vascular system of six-row ears is similar to that of two-row barley ears (Kirby & Rymer, 1974).

7.4 Conclusions

The number of grains per unit area is the most important component of yield; it is determined largely by the number of ears per unit area in two-row cultivars and by the number of grains per ear in six-row types. Differences in 1000 grain weight within a variety can give yield responses up to 1.5 tonnes per hectare (Gallagher, Biscoe & Scott, 1975), and were the main cause of the higher yield in the later sowing in 1981-82.

Tillering in a crop may be preferred to a high plant population, as it maintains a flexible response to the environment, and by producing a broader peak to maximum GAI it increases the amount of PAR absorbed.

Winter sown barley initiates more tiller buds than spring sown barley due to its longer vegetative period. As tiller growth is controlled by the supply of nutrients and assimilate, the first tiller did not necessarily emerge at a certain leaf stage but could be delayed by severe weather. The response to a low plant population was not to increase the rate of tillering but the duration of tillering. The main advantage of the longer duration of tillering due to early sowing or low plant populations, is the increased size and autonomy of initial tillers by the start of mainstem elongation.

Differences in the tillering behaviour of six-row and two-row cultivars are slight before mainstem elongation. Differences in ear population between the two types were due to the greater degree of apical dominance exhibited by the six-row cultivars during mainstem elongation, which gave low tiller survival rates.

Later sowings generally produced fewer spikelet primordia on the mainstem because their faster crop development was not completely compensated by a faster rate of primordia initiation. It was not possible to distinguish whether the faster development and initiation per degree day in later sowings was caused by higher temperatures, longer photoperiods, or a combination of both. Varieties differ considerably in response to these environmental controls.

The number of viable florets at anthesis was more dependent upon the proportion of spikelets aborted, than upon maximum spikelet numbers. The percentage survival of spikelet primordia was positively correlated with the combined area of leaf 2^t and leaf 3^t which were the main light intercepting organs on the mainstem during the period of spikelet death. Further work is required to determine whether this relationship is causal, and if it is, the factors which determine the size of leaf 2^t and leaf 3^t need to be investigated.

Florets which failed to fertilise at anthesis, further reduced grain number, particularly in the six-row cultivar Athene. Sterility of the lower florets could be related to the smaller flag leaf area of Athene. Other workers have suggested that sterile florets are related to poor synchronisation of the flowering events in winter barley rather than any specific environmental stress at flowering (Sage & Roffey, 1983). However, the problem of sterile florets in winter barley cultivars remains unresolved and requires further work to determine its cause, whether it is related to poor synchronisation of flowering, or if pollination is disrupted by stress earlier in development. The recorded reductions of potential grain numbers by 5 to 20 per cent, due to floret sterility must have reduced yield considerably.

It is now generally accepted that the potential size of a barley grain is determined by the time of anthesis (Scott *et al.*, 1983). Controversy remains over whether this potential is normally fulfilled in field crops or if grain size is limited by conditions after anthesis (Gallagher, Biscoe & Scott, 1975 ; Thorne, 1974; Gallagher, 1979b Stoy, 1980). High temperatures, decreased PAR, or drought, during grain filling can reduce grain size (Welbank, Witt & Thorne, 1968; Jenner, 1979; Lawlor *et al.*, 1981). However, assimilate supply to the ear is partially dependant upon sink demand (Wardlaw & Moncur, 1976). In the present study: grain size was not increased in S81 despite higher levels of absorbed PAR and unused stem reserves; the presence of sterile florets did not influence the size of neighbouring grains; and maximum grain weight on the mainstem was positively correlated with floret size at anthesis. Hence, the potential grain size appears to have been fulfilled.

The potential grain size may be fulfilled in most barley crops in South East Scotland where the grain filling period is cool (mean daily temperatures $\simeq 14^{\circ}C$), coupled with high levels of available PAR, and the possibility of mobilising stem reserves. This conclusion is partially supported by the work of Dyson on spring barley in North East Scotland, where grain yield was more closely related to crop dry weight at ear emergence than to any subsequent increase in weight (Dyson, 1977).

Further work is required to determine whether the relationship between floret size and final grain weight is causal. If it is, the factors which determine floret size need to be investigated.

Many of the tillers and spikelets produced by winter barley varieties are later aborted. If a genotype were available in which development was such that the maximum number of tillers and spikelets was reached sometime before rapid crop growth begins at stem elongation, then assimilate which would have been used in initiating non-productive tillers and spikelets, would instead be utilised for tiller and spikelet growth, thus enhancing their chances of survival. Less is known about the control of development in winter barley than almost any other facet of its physiology relating to yield, yet it exercises control over the duration of growth and the partitioning of dry matter to various organs. It is an area which requires much further study.

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